

ASPECTS OF THE MORPHOLOGY OF THE ENDEMIC
SOUTH AFRICAN CYPRAEIDAE WITH A DISCUSSION OF THE
EVOLUTION OF THE CYPRAEACEA AND LAMELLARIACEA

By

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(With 35 figures and 1 table)

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ABSTRACT

Aspects of the morphology of eight endemic species of South African Cypraeidae are studied and the variability of various characters within the family is discussed. Lack of knowledge at present prevents the subdivision of *Cypraea* into monophyletic genera or subgenera. A discussion of the phylogeny of the Cypraeacea and Lamellariacea confirms that the Triviidae are allied to the Lamellariidae rather than the Cypraeidae and Ovulidae. Examination of *Pedicularia californica* reveals that it is most closely allied to the Ovulidae. The three species of South African Cypraeidae that have been studied exhibit direct development and lack a free-swimming veliger larva.

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INTRODUCTION

The family Cypraeidae is one of the most widely studied groups of molluscs, yet surprisingly little is known about its morphology and biology. The vast amount of systematic work within the Cypraeidae has been based largely on conchological features with little attempt to correlate these with characters of the

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living animal, radula, or internal morphology of the nervous and reproductive systems. The shores of southern Africa are rich in *Cypraea* species, and are particularly noteworthy owing to the large number of endemic species. Burgess (1970) listed ten endemic species from southern Africa. Since then *Cypraea cruickshanki* Kilburn, 1972, *C. iutsui* (Shikama, 1974), *C. lisetae* Kilburn, 1975, and *C. connelli* Liltved, 1983, have been described, although the validity of some of these species has been questioned. *Cypraea broderipi* has more recently been found from Somalia (Derry 1981), Mauritius and Réunion Island (Whatmore 1981) and can no longer be considered endemic. Morphological studies of the endemic species of South African *Cypraea* are limited to the illustration of the radulae of *C. fultoni* and *C. capensis* (Kilburn & Aiken 1972), *C. iutsui* (Barnard 1963, as globose form of *C. fuscrobura*) and *C. cruickshanki* (Kilburn, 1972), and a brief description of the female reproductive system of *C. capensis* (Kilburn & Aiken 1972).

Recent collections, by means of SCUBA diving along the South African coast from the Cape Peninsula to Algoa Bay, have yielded living specimens of five additional species of *Cypraea*. Their morphology is described here together with that of preserved specimens of *C. capensis*, *C. cruickshanki* and *C. iutsui*. The taxonomic status of the South African endemic Cypraeidae is reviewed.

Many authors (e.g. Schilder 1936) have suggested that *Cypraea* be subdivided into numerous genera or subgenera while others have maintained that the species should remain united within a single genus. The relative strengths and weaknesses of these arguments are presented.

There has also been considerable question as to the relationships of the various families comprising the Cypraeacea and Lamellariacea, particularly regarding the status of the Triviidae and *Pedicularia*. The morphology of these taxa is reviewed and the phylogeny of these superfamilies is discussed.

MORPHOLOGICAL DESCRIPTIONS

Cypraea fuscrobura Shaw, 1909

Figs 1A, 2–8, 33A

Cypraea similis Gray, 1831: 36, non Gmelin, 1791.

Cypraea fuscrobura Shaw, 1909: 302.

Cypraea gondwanalandensis Burgess, 1970: 31, pl. 1 (figs A–A2).

Material

Specimens (SAM–A35990) were collected at several localities on the Atlantic coast of the Cape Peninsula from 25 to 48 m depth. A single specimen (SAM–A35991) was collected from Danger Point in 30 m of water.

Distribution

Cypraea fuscrobura is known from the Atlantic coast of the Cape Peninsula to Cape Agulhas.

Shell

The shell (Fig. 2) is ovoid, 28–40 mm in length. The spire is generally not umbilicate and the protoconch is generally covered by a callus. The labrum has a dull finish with 17–18 coarse brown teeth. The aperture is moderately narrow, widest anteriorly. The columella has 18–24 teeth, which are finer than the labral teeth and do not extend beyond the aperture. The fossula is straight to convex with three or four denticles. The dorsum is thickly calcified. The dorsal surface is cream, slate-grey or mauve and is densely spotted with a reticulate pattern of spots. The base is thick, cream in colour with brown spotting.

Living animal (Fig. 1A)

The foot is thick and wide, shortened and rounded posteriorly. The foot and siphon are white in colour and their dorsal surface may be ornamented with sparse black spots or stippling. The smooth siphon is short and wide, recurved and slightly uneven at the apex. The yellow tentacles are straight and slightly tapered. The opaque mantle is smooth but occasionally it has a slightly granular texture. Typically the ground-colour of the mantle is red or whitish but occasionally it may be cream with black longitudinal lines forming a 'finger-print' pattern of parallel lines.

Mantle complex (Fig. 3)

The mantle cavity is directed towards the right side of the body. The ctenidium is large, consisting of approximately 200 triangular plicae. The triradiate osphradium is situated anterior to the ctenidium and consists of numerous leaflets. Posterior to the ctenidium, on the left side of the body, is the vascular kidney. At the junction of the ctenidium and kidney is the two-chambered heart. Near the opening of the mantle cavity, at the level of the kidney, is the hypobranchial gland, which consists of 11 plicae.

Digestive system

The large, muscular buccal mass comprises the bulk of the anterior portion of the body (Fig. 4). From it extend the wide, glandular oesophagus and the coiled radular sac. The salivary glands are fused and possess a pair of ducts that pass through the nerve ring and the buccal mass adjacent to its junction with the oesophagus. The oesophagus narrows into the intestine, which forms a short loop, the stomach. There are two ducts emanating from the stomach to the large, granular digestive gland. No caecum was observed. The intestine curves to the right beyond the stomach and terminates at the anus, near the opening of the mantle cavity (Fig. 3).

The buccal mass contains a pair of flexible jaws (Fig. 5), which almost completely dissolve when placed in 10 per cent sodium hydroxide. The taenioglossate radula is a narrow, elongate ribbon, about two-thirds of which is contained within the radular sac at the posterior end of the buccal mass. The

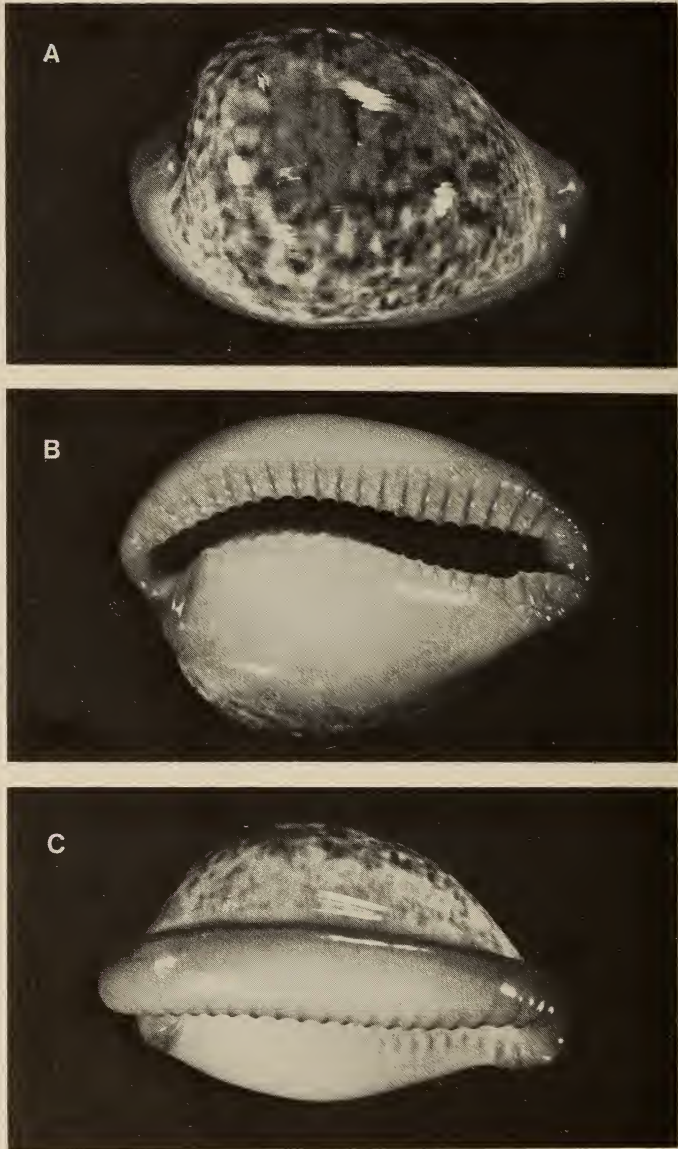


Fig. 2. *Cypraea fuscrobura* Shaw, 1909. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

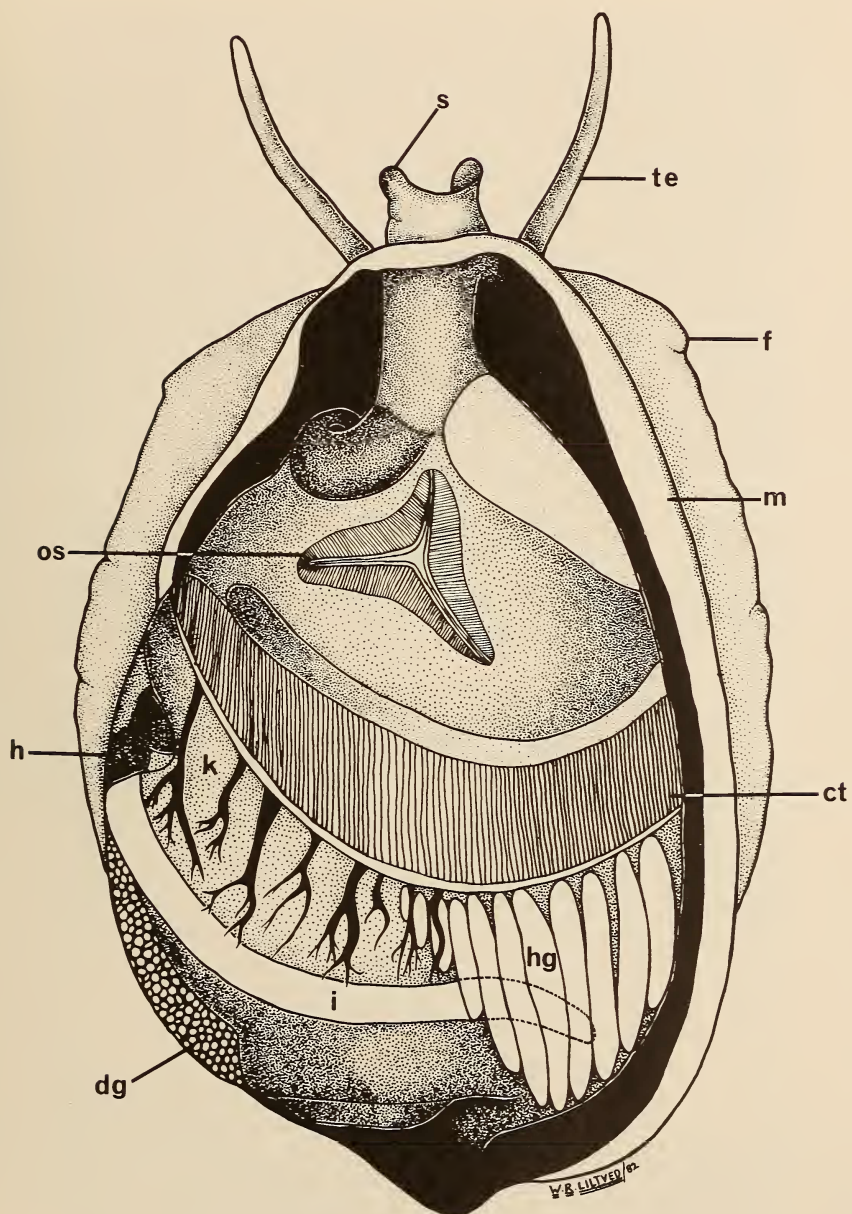


Fig. 3. *Cypraea fuscorubra* Shaw, 1909. Mantle complex.

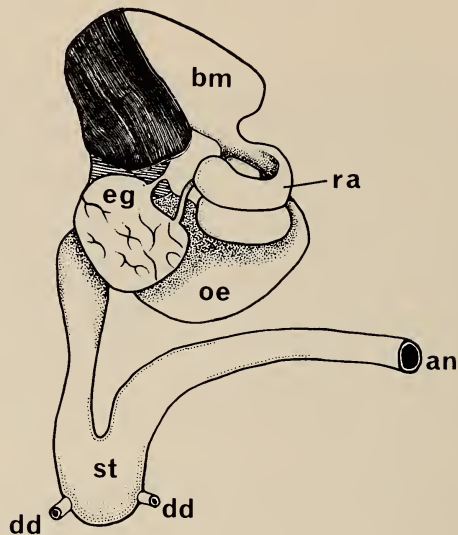


Fig. 4. *Cypraea fusciorubra* Shaw, 1909.
Digestive tract.

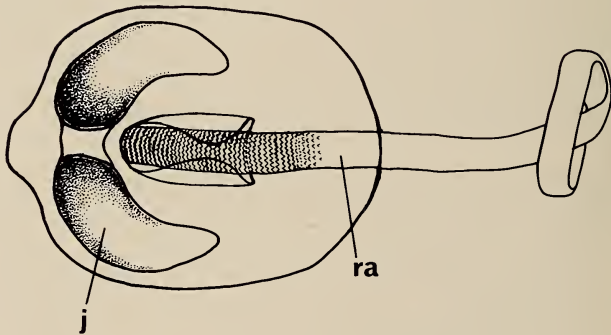


Fig. 5. *Cypraea fusciorubra* Shaw, 1909. Jaws.

radula (Figs 6, 33A) consists of 93–96 rows of teeth. Each row contains three lateral teeth on either side of the rachidian tooth. Each tooth has a small rounded denticle on either side of the strong central cusp. There is a thin outer margin and a strong, centrally emarginate base to the rachidian tooth.

Central nervous system (Fig. 7)

The central nervous system is modified from the typical prosobranch plan. It is highly cephalized and asymmetrical with most ganglia situated to the left of the oesophagus. The paired cerebral ganglia are closely appressed to each other,



Fig. 6. *Cypraea fusciorubra* Shaw, 1909. Scanning electron micrographs of teeth. A. Entire width of radula. B. Central region.

without a distinct commissure between them. From the cerebral ganglia a pair of nerves emanates anteriorly and joins the paired buccal ganglia on either side of the junction of the oesophagus and buccal mass. Adjacent and slightly dorsal to the cerebral ganglia are the pleural ganglia. From their anterior side a pair of nerves connects with the supraintestinal ganglion, situated anterior to the cerebral ganglion at the base of the osphradium, on the left side of the mantle cavity. The nerve between the left pleural and supraintestinal ganglia represents a zygoneurous connective. Nerves from the supraintestinal ganglion innervate the osphradium and ctenidium, and extend to the posterior end of the body cavity. From the posterior side of the cerebral and pleural ganglia extend the pedal connectives, which are fused for most of their lengths. The pedal connectives join the elongate pedal ganglia, which are fused anteriorly without a distinct commissure. These ganglia are embedded in the muscular tissue of the foot. There are nerves emerging from the outer side of most of the length of the pedal ganglia and ladder-like connectives between the two ganglionic masses. A thick, elongate nerve emerges from the posterior end of the left pleural ganglion and

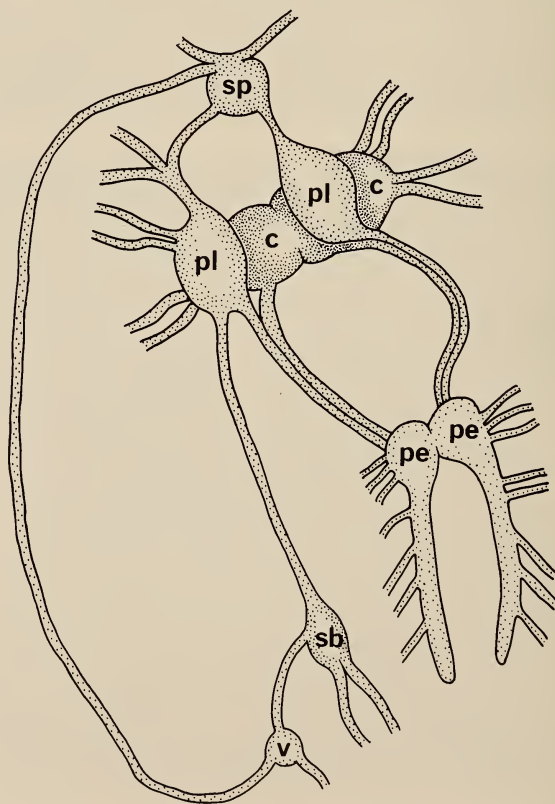


Fig. 7. *Cypraea fuscorubra* Shaw, 1909.
Central nervous system.

joins the subintestinal ganglion near the posterior end of the body cavity. Three large nerves emerge from the posterior portion of the subintestinal ganglion. The nerve at the left side of the ganglion continues posteriorly and connects with the small visceral ganglion, at the base of the genital mass, near the posterior limit of the oesophagus. The visceral ganglion branches posteriorly to innervate the genital mass and anteriorly gives rise to the right lateral nerve cord, which continues anteriorly until it joins the suprainintestinal ganglion.

Reproductive system

The animals are gonochoric. The female system (Fig. 8A) consists of a large, yellowish ovary, which interdigitates with the digestive gland. From the anterior

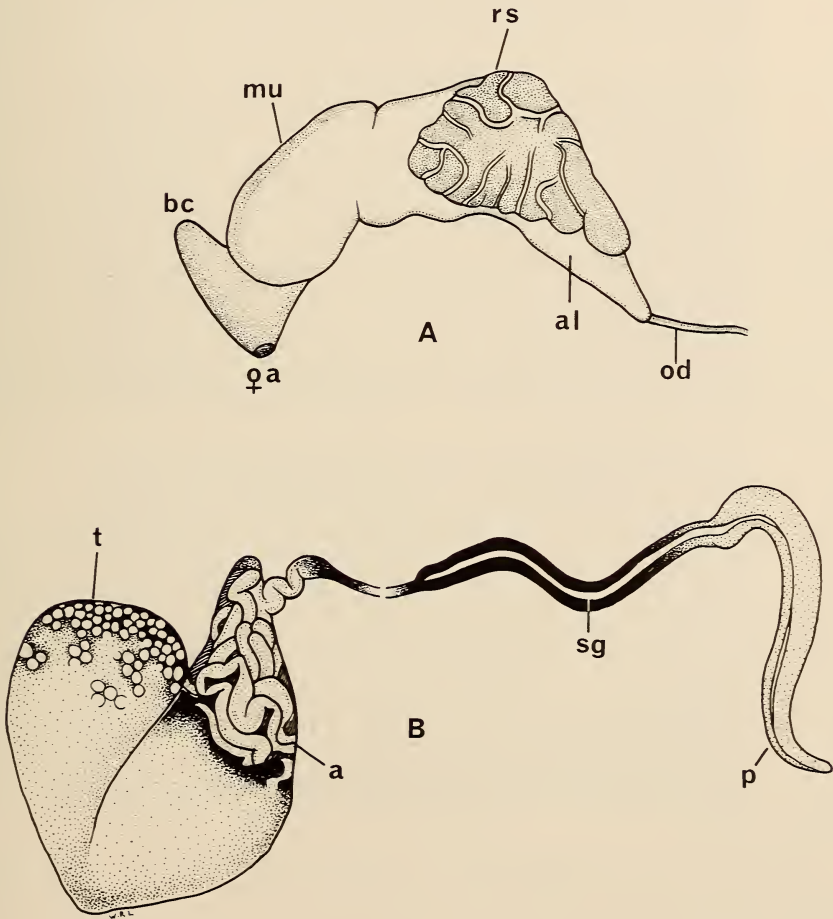


Fig. 8. *Cypraea fuscorubra* Shaw, 1909. A. Female reproductive system.
B. Male reproductive system.

end of the ovary the narrow oviduct emerges. It widens into the albumen gland. On the anterodorsal surface of the albumen gland is the dark grey, glandular receptaculum seminis. Ventral to the receptaculum seminis is the narrow band of the membrane gland. Anteriorly, the bulk of the female gland mass is composed of the mucous gland (= capsule gland of Kay (1960*b*)). The mucous gland narrows anteriorly and joins the bulbous bursa copulatrix near the gonopore.

The male system (Fig. 8B) consists of a large testis with numerous acini. These empty into the elongate, highly convoluted ampulla (= seminal vesicle of Kay (1960*b*)). The ampulla narrows to a glandular, prostatic vas deferens with an opening near the entrance of the mantle cavity. From this opening a ciliated sperm groove connects the vas deferens to the tip of the muscular penis on the right side of the head.

Cypraea algoensis Gray, 1825

Figs 1B, C, H, 9–11, 32, 33B

Cypraea algoensis Gray, 1825: 498.

Material

Numerous specimens have been collected and studied from 20 to 48 m depth along the Atlantic coast of the Cape Peninsula (SAM-A35992), in 17–35 m depth in False Bay (SAM-A35993), and recorded from 30 m depth at Danger Point.

Distribution

Specimens have been collected along the south-western Cape coasts from Saldanha Bay on the Atlantic coast to Cape Agulhas. This species may extend as far north-east as Jeffreys Bay.

Shell

Conchologically *Cypraea algoensis* is variable but with some consistent and distinctive features. The adult shell (Fig. 9) ranges from 12 to 31 mm in length. The spire is generally not umbilicate and the protoconch may or may not be visible. The labrum is strongly developed with 14–21 fine white teeth, which extend across about half the width of the labrum. The narrow aperture is widened anteriorly and strongly curved posteriorly. There are 9–21 finely denticulate columellar teeth. The fossula is poorly developed or absent, occasionally with two or three denticles. The shell varies in shape from pyriform to globular. Globose specimens are generally characteristic of water deeper than 50 m, and are more heavily calcified.

Shells from the Atlantic coast of the Cape Peninsula are generally about one-third larger and have a flesh or orange ground-colour with fine brown dorsal spotting, while shells from False Bay to Cape Agulhas are normally smaller and may be dark purple with dark brown dorsal spots. The base of the shell and the teeth are always whitish and dark brown marginal spots are present.

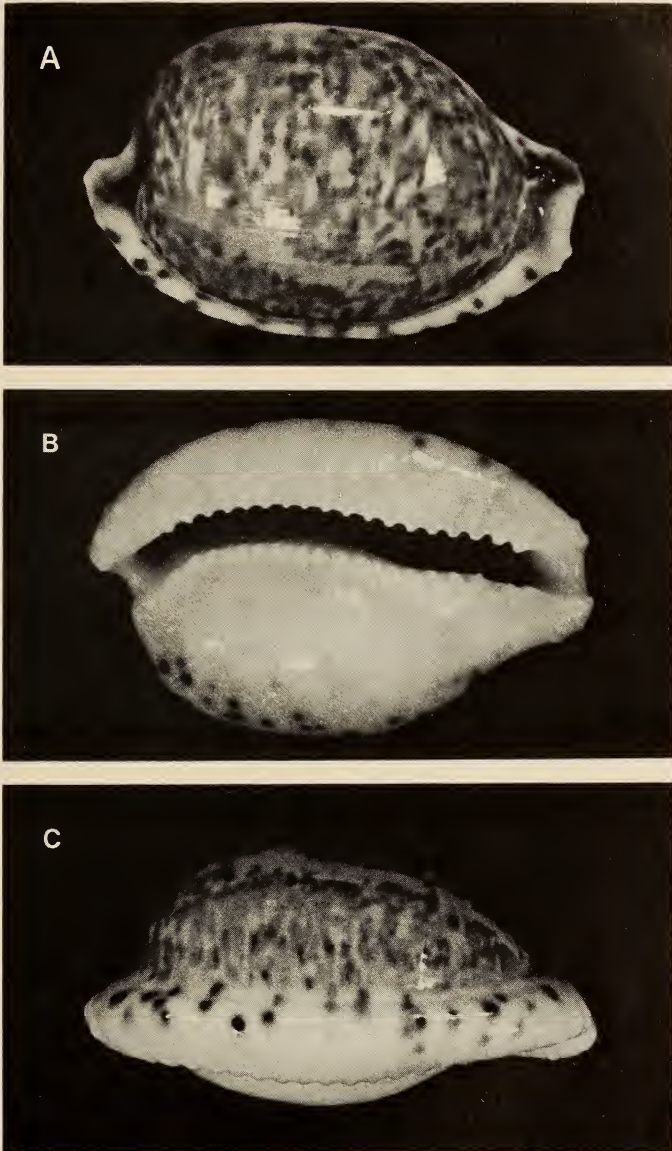


Fig. 9. *Cypraea algoensis* Gray, 1825. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

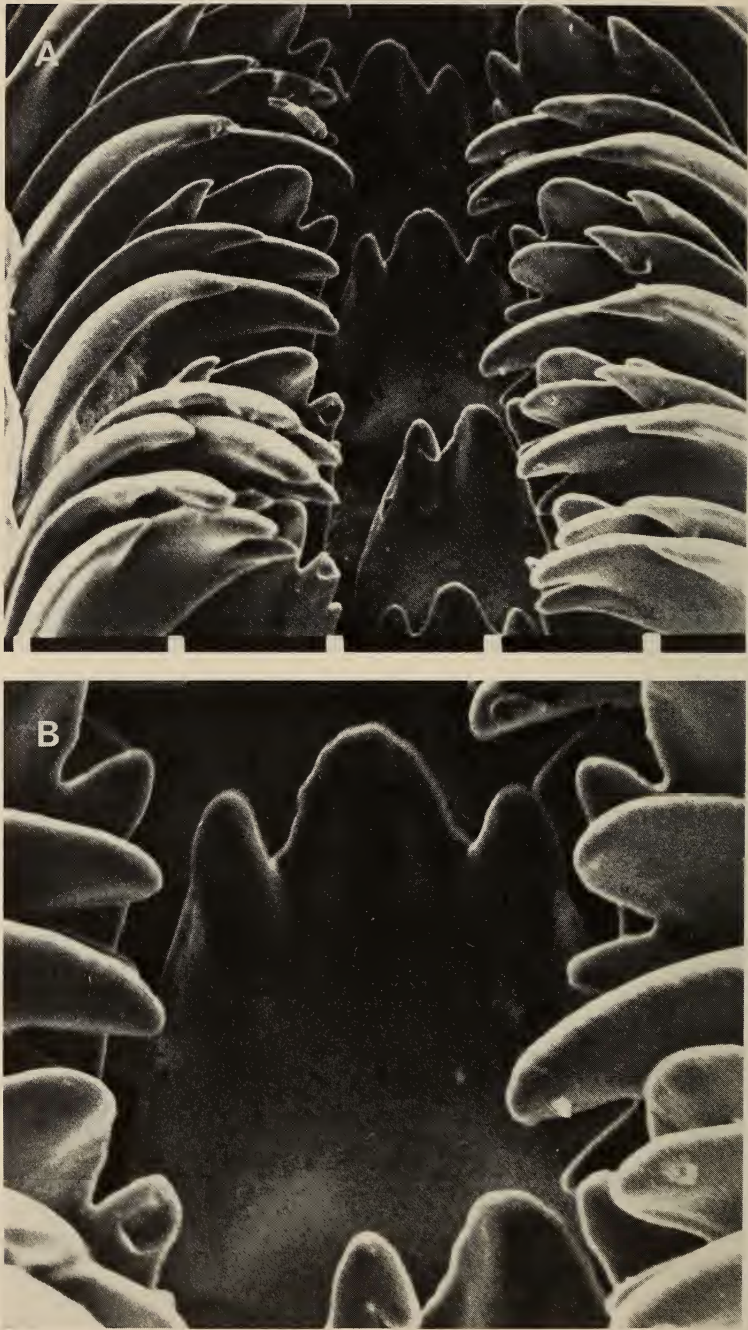


Fig. 10. *Cypraea algoensis* Gray, 1825. Scanning electron micrographs of radula. A. Entire width. B. Central region.

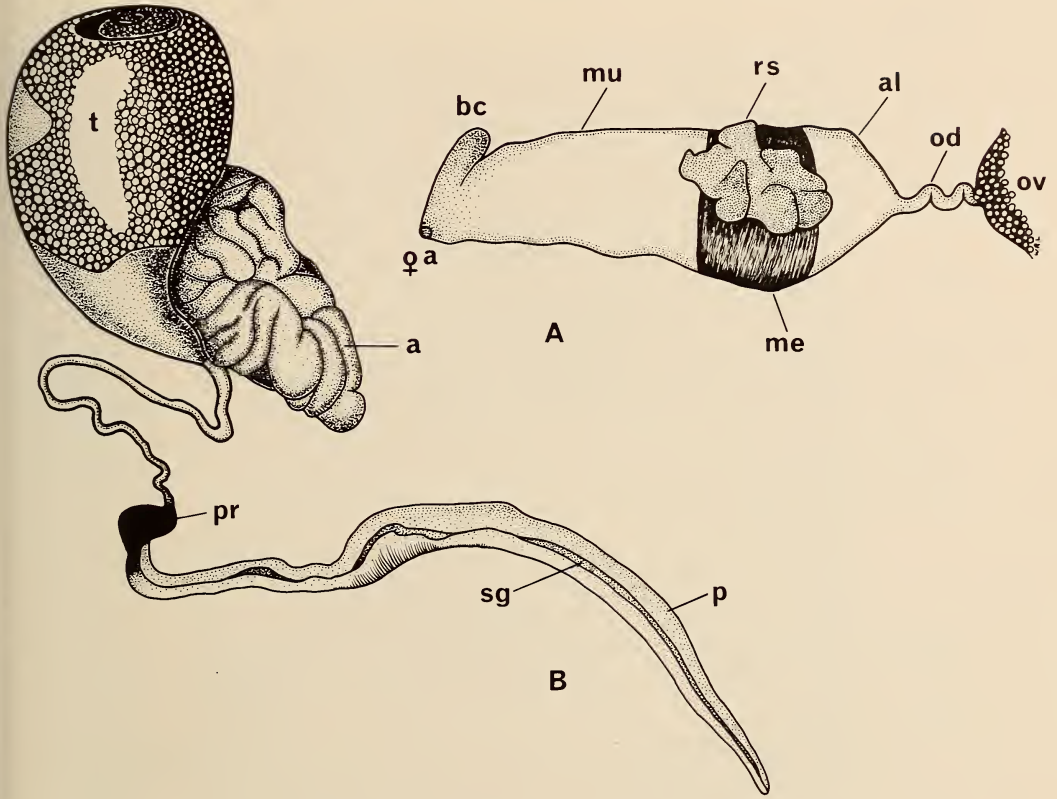


Fig. 11. *Cypraea algoensis* Gray, 1825. A. Female reproductive system. B. Male reproductive system.

Living animal (Fig. 1B, C)

The foot is short and thick, rounded posteriorly. Most commonly the foot is salmon-pink in colour but it may occasionally be white, and black spots may be present. Specimens from False Bay generally possess a dense pattern of black lines. The smooth siphon is white or black with a white apex; the tip is slightly thickened but smooth. The lemon-yellow tentacles are slender and slightly tapered. The mantle is salmon or translucent white, with finely stippled black specks, or marked with fine brown lines forming a 'finger-print' pattern. Specimens from False Bay to Cape Agulhas generally have a black mantle, which often possesses white wart-like or fleshy finger-like papillae.

Mantle complex

The arrangement of organs within the mantle complex is identical to that described for *C. fuscobrunna*. The ctenidium consists of about 150 leaflets while the hypobranchial gland is composed of seven plicae.

Digestive system

The digestive organs are arranged as in *C. fuscorubra*. The radular formula is 77–91 × 3.1.3. The rachidian tooth (Figs 10, 33B) is broad and rectangular with a small central cusp flanked by a pair of oblong cusps. The base of the rachidian tooth is short with a slight medial indentation. The lateral teeth are also broad with three cusps. The central cusp is shortest on the inner lateral tooth and longest on the outermost.

Central nervous system

The arrangement of ganglia is identical to that described for *C. fuscorubra*.

Reproductive system

The configuration of both the male and female reproductive organs is similar to that described for *C. fuscorubra*. The only significant differences are the proportionately smaller receptaculum seminis in the female (Fig. 11A) and the discrete prostate in the male of *C. algoensis* (Fig. 11B).

Cypraea coronata (Schilder, 1930)

Figs 1D–E, 12–15, 33C

Luponia coronata Schilder, 1930: 113, text-fig.

Cypraeovula gloriosa Shikama, 1971: 101.

Material

Five specimens (SAM–A35988) were examined from the Atlantic coast of the Cape Peninsula where they were collected in 25–48 m of water. A single specimen was also recorded from 30 m depth off Danger Point.

Distribution

Cypraea coronata is known from the Atlantic coast of the Cape Peninsula to Transkei.

Shell (Fig. 12)

The shell varies in length from 26 to 36 mm and is pyriform with closely spaced growth lines. The spire is slightly umbilicate with a well-developed callus covering the protoconch. The prominent labrum and thickened columellar margin are tuberculate. Tubercles may be absent in juvenile specimens and occasionally in adults. The aperture is narrow, widening slightly anteriorly and curving posteriorly. There are 18–20 coarse teeth on the labrum, some of which are occasionally fused. The anteriormost and posteriormost teeth may extend over the labrum and fuse with the tubercles. There are 16–22 columellar teeth. The mid-columellar teeth are fine and become coarser and pigmented towards either end of the columella. These anterior and posterior columellar teeth extend on to the columella. The dorsal surface of the shell is mauve, slate-grey or cream with transverse rows of olive-green or brown pigment. This pigment is usually

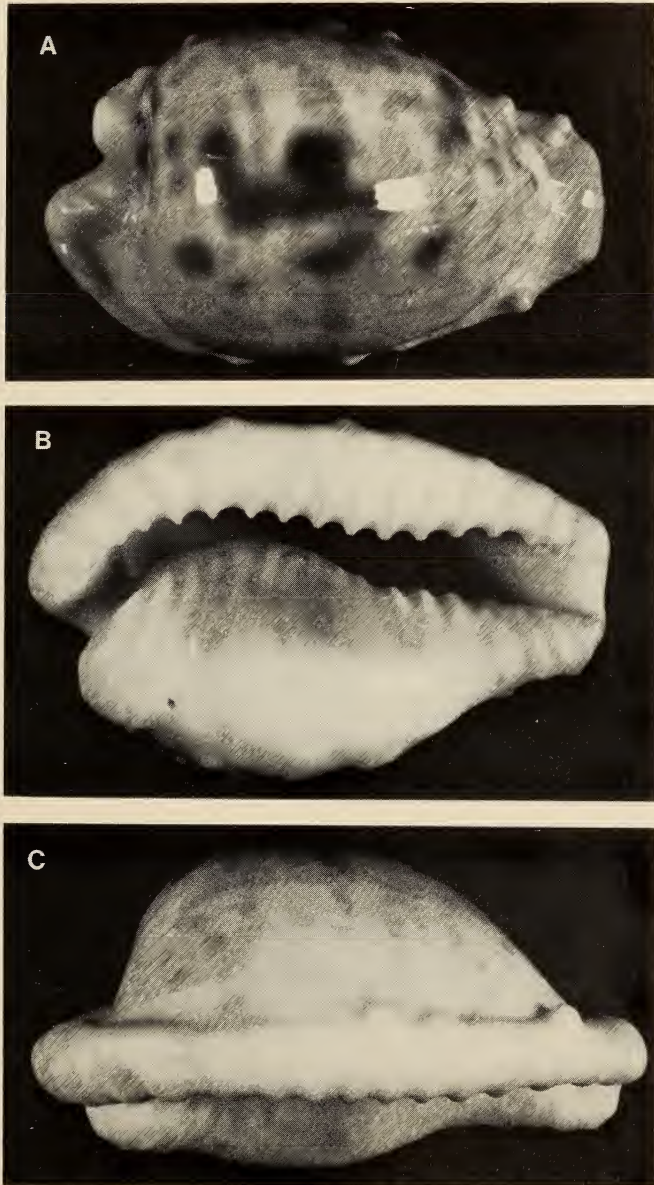


Fig. 12. *Cypraea coronata* (Schilder, 1930). Shell. A. Dorsal aspect.
 B. Ventral aspect. C. Lateral aspect.

overlaid with blotches of olive-green or chestnut-brown, which may cover most of the dorsal surface of the shell.

Living animal (Fig. 1D-E)

The external morphology of *Cypraea coronata* is less variable intraspecifically than in any other species of endemic Cypraeidae in southern Africa. The creamy-white foot is thick, short and fleshy. It is thickened anteriorly. The siphon is usually sparsely papillate throughout with minute wart-like papillae, and is thickened at its tip. The lemon-yellow tentacles are slender and gradually taper; the tips are blunt and slightly darker in colour. The mantle is covered with white wart-like papillae approximately 1 mm in diameter. Between these papillae are more numerous smaller papillae about 0,2 mm in diameter. The margins of the mantle lobes are covered with a reticulate pattern of dark-brown or black pigment. This pigment does not extend on to the surface of the papillae. The intensity of the pigment decreases away from the margins of the lobes and is replaced by pink pigment. Specimens with a black or translucent white mantle and white papillae have been encountered but are rare.

Mantle complex

The arrangement of organs within the mantle complex is identical to that described for *C. fuscorubra*. The ctenidium consists of approximately 200 leaflets while the hypobranchial gland contains four plicae.

Digestive system

The only significant feature of the digestive system distinguishing *C. coronata* from *C. fuscorubra* is the morphology of the radula. The radular formula is $95 \times 3.1.3$ in one specimen examined. The rachidian teeth (Figs 13, 33C) are square in shape rather than trapezoidal. The central cusp is triangular and is flanked by a pair of rounded lateral denticles. At the base of each of the lateral denticles is a small secondary denticle. The base of the rachidian tooth is small and medially slightly emarginate. The lateral teeth (Fig. 14) also possess a pair of primary denticles on either side of the elongate central cusp and a secondary cusp at the base of the inner primary denticle of the first two laterals. The bases of the lateral teeth are proportionately smaller than in *C. fuscorubra*.

Central nervous system

The configuration of the ganglia is identical to that described for *C. fuscorubra*.

Reproductive system

The male system is identical to that described for *C. fuscorubra*. The female system (Fig. 15) is only slightly different; the receptaculum seminis of *C. coronata* appears to be more ramified than that of *C. fuscorubra*.

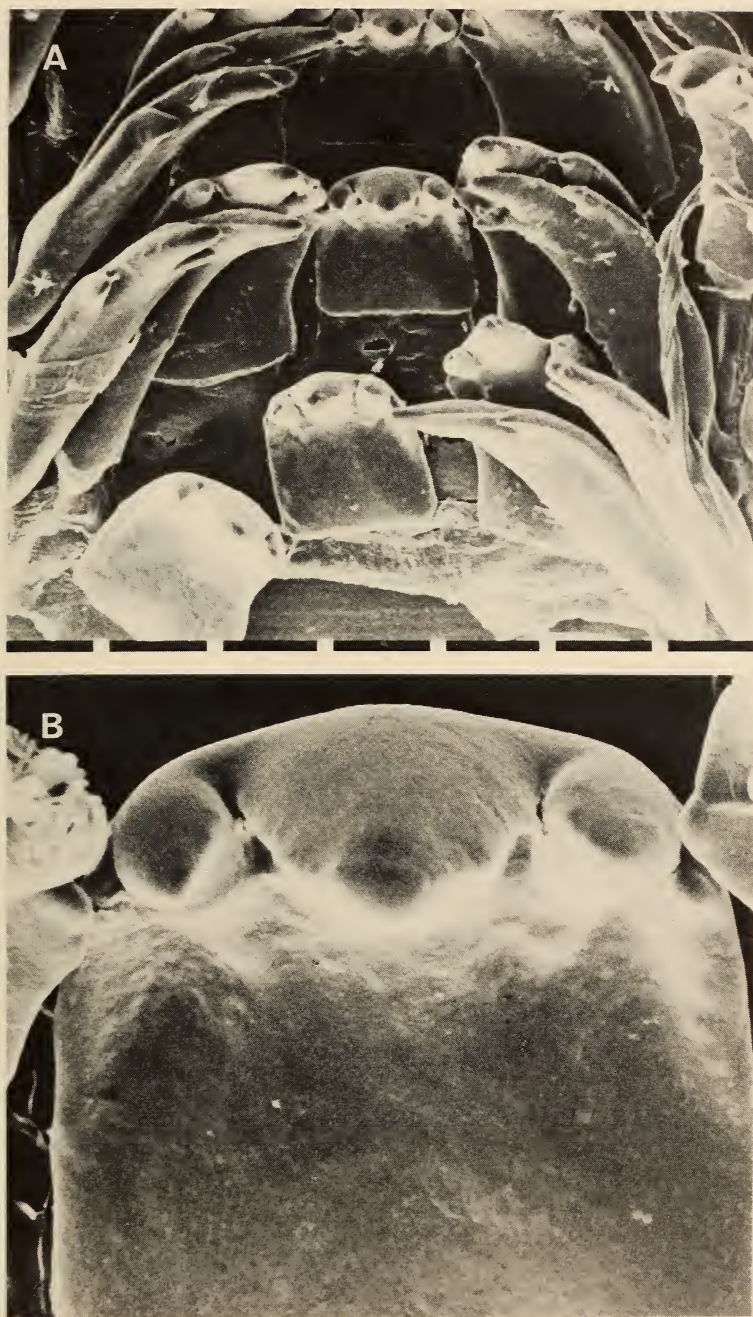


Fig. 13. *Cypraea coronata* (Schilder, 1930). Scanning electron micrographs of radula. A. Entire width. B. Rachidian tooth.



Fig. 14. *Cypraea coronata* (Schilder, 1930). Scanning electron micrograph of inner lateral tooth.

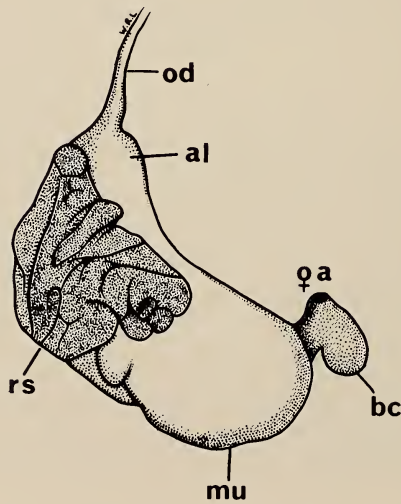


Fig. 15. *Cypraea coronata* (Schilder, 1930). Female reproductive system.

Cypraea fuscudentata Gray, 1825

Figs 1F, 16–18, 33D

Cypraea fuscudentata Gray, 1825: 499.*Material*

Ten specimens (SAM–A35989) were collected from 6 to 35 m in False Bay, Cape Peninsula.

Distribution

Cypraea fuscudentata has been collected from False Bay to Jeffreys Bay.

Shell

The shell (Fig. 16) is cylindrical to pyriform, ranging in length from 21 to 44 mm. The spire is umbilicate and the protoconch is generally obscured. The labrum has 15–19 coarse, dark-brown teeth. The aperture is very narrow. The 15–20 coarse columellar teeth extend from the aperture across most of the width of the columella. The fossula is straight or convex, without denticulations. The dorsal surface is thickly calcified with a cream or grey ground-colour and a dense pattern of brown spots. The margins of the shell may be cream, brown or purple.

Living animal (Fig. 1F)

The broad foot is short and posteriorly rounded. The siphon is recurved at the smooth tip and may be white or black with a white tip. The tentacles are elongate and slightly tapered, and yellow to orange in colour. The coloration of the mantle and foot is exceedingly variable. It may be black, white, orange, brown or red in individuals from the same population. Sparse papillae of variable shape may be present or absent from the outer surface of the mantle. When present the papillae tend to be denser near the margins of the mantle.

Mantle complex

The organs of the mantle cavity are arranged identically to those described for *C. fuscubra*. In a juvenile specimen the ctenidium consists of about 150 leaflets and the hypobranchial gland of seven plicae.

Digestive system (Figs 17, 33D)

The organs of the digestive system are arranged identically to those described for *C. fuscubra*. The rachidian tooth of *C. fuscudentata* has a pair of distinct ridges on the inner face, which are absent in *C. fuscubra* and *C. coronata*. The radular formula in one specimen is $83 \times 3.1.3$. The central cusp is short, as are the oblong adjacent cusps. The central cusp of each of the lateral teeth is elongate, as are the smaller adjacent cusps.

Central nervous system

The arrangement of ganglia is identical to that of *C. fuscubra*.

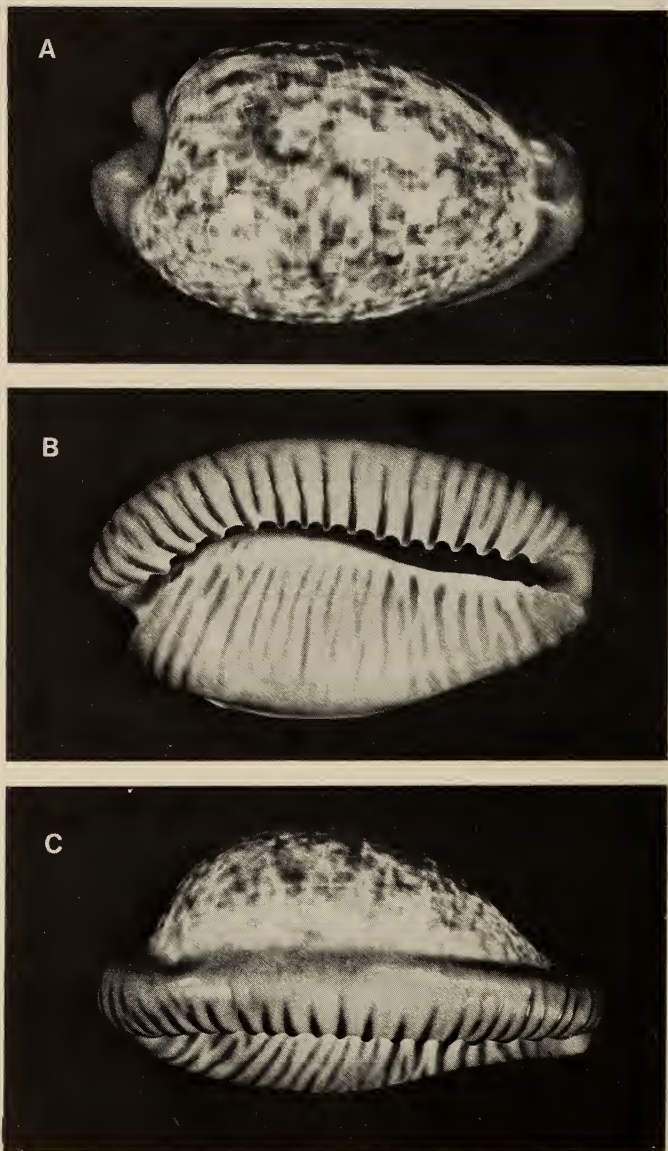


Fig. 16. *Cypraea fuscodentata* Gray, 1825. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.



Fig. 17. *Cypraea fuscodentata* Gray, 1825. Scanning electron micrographs of radula. A. Entire width. B. Central region.

Reproductive system

Both the female and male systems are arranged in the manner described for *C. fusciorubra* with the exception that the receptaculum seminis is far more elaborate in *C. fuscodontata* (Fig. 18).

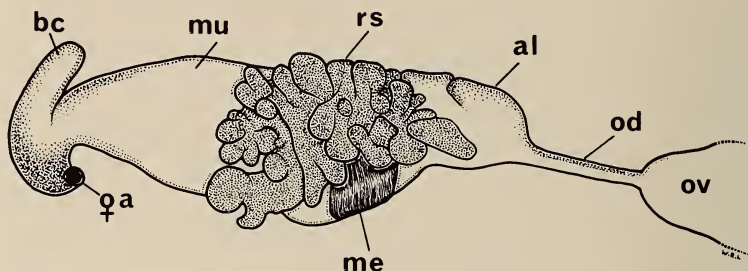


Fig. 18. *Cypraea fuscodontata* Gray, 1825. Female reproductive system.

Cypraea capensis Gray, 1828

Figs 19–20, 33E

Cypraea capensis Gray, 1828: 573.

Material

The single specimen (SAM–A35995) examined was removed from the stomach of a fish collected in Algoa Bay.

Distribution

Cypraea capensis is known from the eastern Cape Province and Transkei from Jeffreys Bay to Port St. Johns, and from deep water off Natal.

Shell (Fig. 19)

The shell is elongate, pyriform, from 22 to 39 mm in length. The spire is umbilicate and the protoconch may be obscured by a callus. The labrum is ornamented with 20–28 fine, brown teeth, which extend on to and across the dorsum and columella as transverse ribs. These ribs continue on to the columella, where they merge with the columellar and fossular denticles. The fossula is convex. The dorsum may be brown, grey or purple in colour, and may or may not be ornamented with dark brown mottling.

Living animal

The only description of the external morphology of *C. capensis* is that of Kilburn & Aiken (1972). In the specimen they described the foot and tentacles were bright orange-yellow and the mantle was brownish with dark spots and faint white lines.

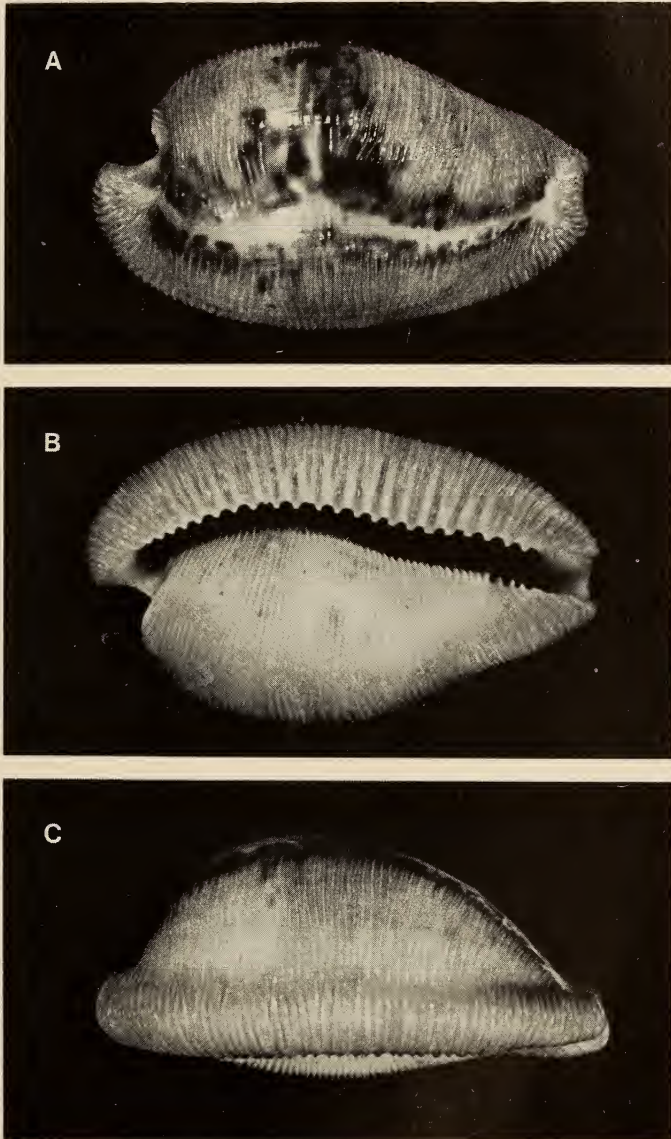


Fig. 19. *Cypraea capensis* Gray, 1828. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

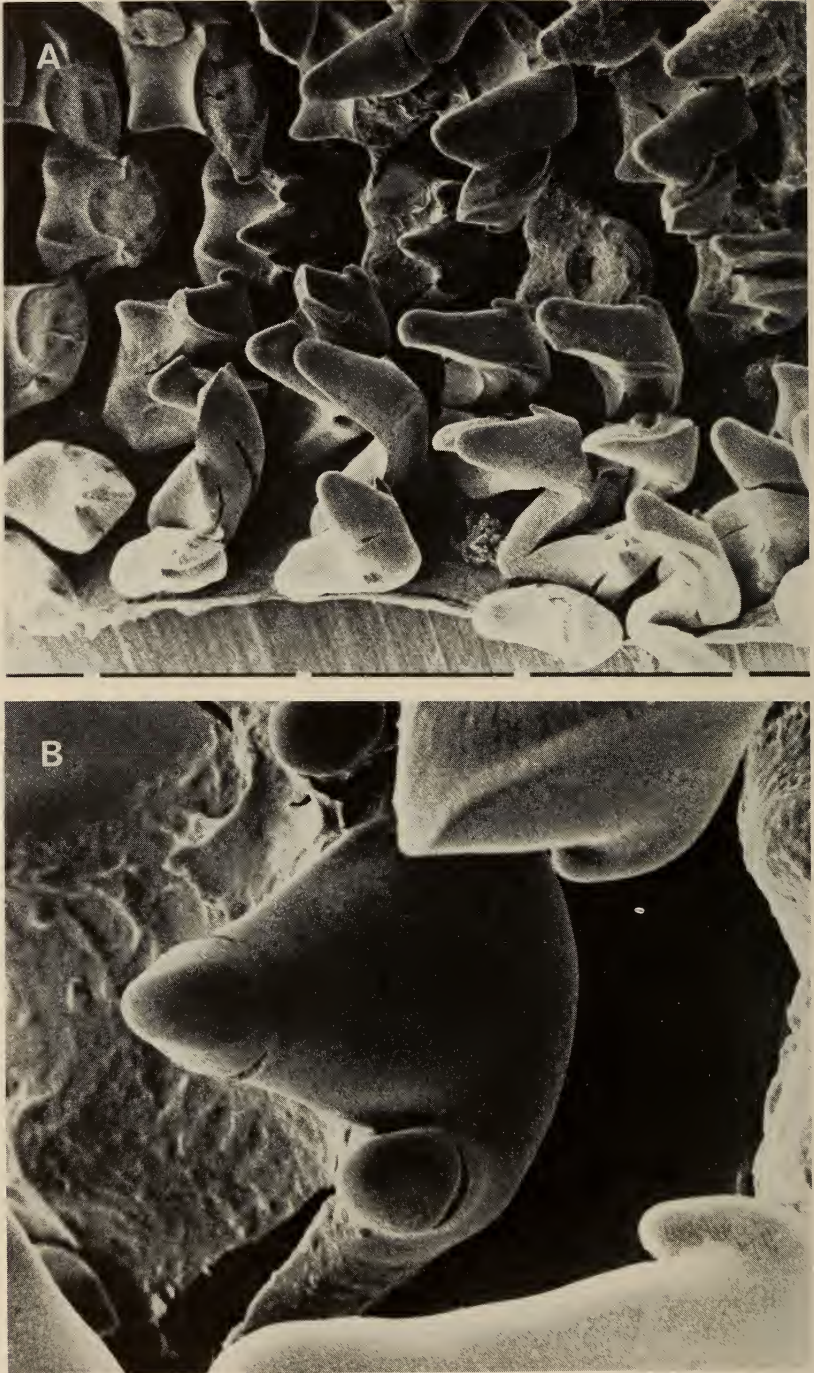


Fig. 20. *Cypraea capensis*. Scanning electron micrographs of radula.
A. Entire width. B. Central region.

Mantle complex

Owing to the desiccation of the specimen details of the mantle complex could not be determined.

Digestive system (Figs 20, 33E)

The radular formula is $76 \times 3.1.3$. The rachidian tooth is trapezoidal with a well-developed triangular central cusp. There is a pair of strong ridges on the inner side of the rachidian tooth. The base of the rachidian tooth is large and deeply emarginate. The lateral tooth possesses an elongate cusp and rounded adjacent denticles.

Central nervous system

Although the specimen was poorly preserved it was possible to determine that there is an elongate lateral nerve cord present between the left pleural and subintestinal ganglia as in *C. fuscorubra*. The pedal ganglia are also elongate.

Reproductive system

The specimen was not sufficiently preserved to examine the reproductive system. Kilburn & Aiken (1972) stated that the female specimen they examined had a glandular receptaculum seminis and a bursa copulatrix. However, it is unclear whether the receptaculum consists of small glands as described by Kay (1960a) or if it is lobate as in the other South African species examined in this study.

Cypraea edentula Gray, 1825

Figs 1G, 21–23, 33F

Cypraea algoensis var. *edentula* Gray, 1825: 498.

Material

One specimen destroyed by dissection was collected off the Sunday's River Mouth north of Port Elizabeth in 48 m of water. A second specimen (SAM-A35994) was collected from 12 m in Algoa Bay.

Distribution

Cypraea edentula has been collected from Tsitsikama Coastal National Park to the south-western Transkei.

Shell (Fig. 21)

The shell of *Cypraea edentula* varies in length from 12 to 33 mm and is highly variable in shape and coloration. The spire may be slightly umbilicate or produced. The protoconch is usually visible. Generally, labral and columellar teeth are entirely absent. Some specimens have poorly-developed denticles on the labrum but these are normally limited to the anterior end and are very faint. The fossula is smooth and convex with as many as six denticles. Typically the shell is

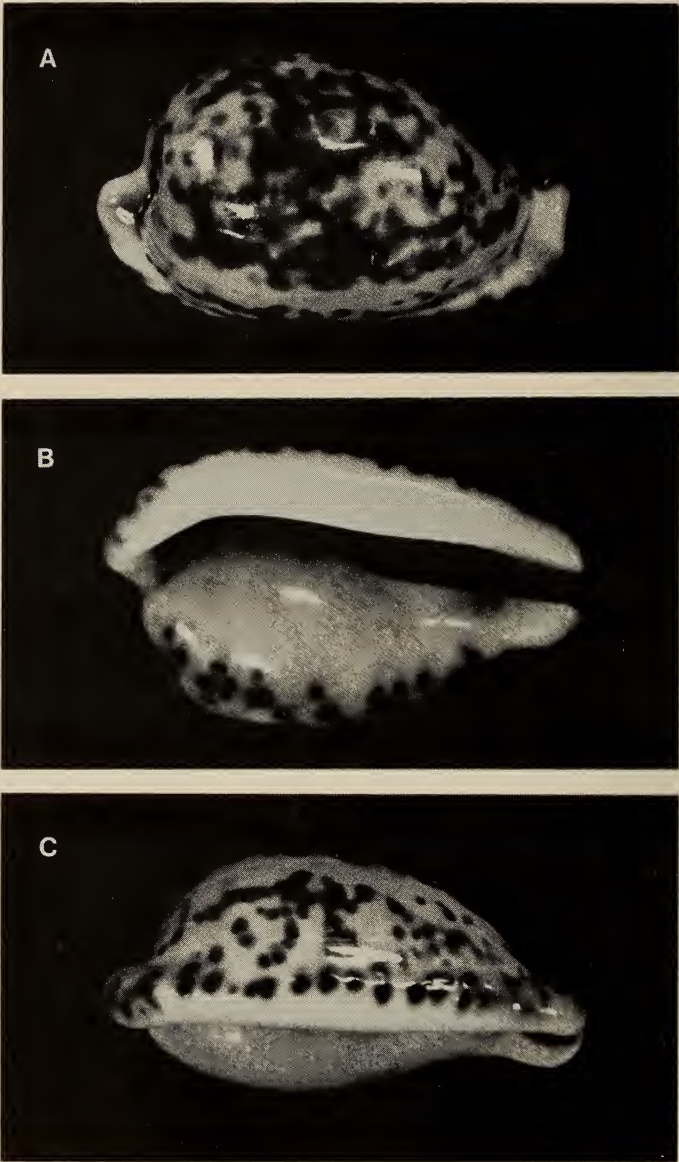


Fig. 21. *Cypraea edentula* Gray, 1825. Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

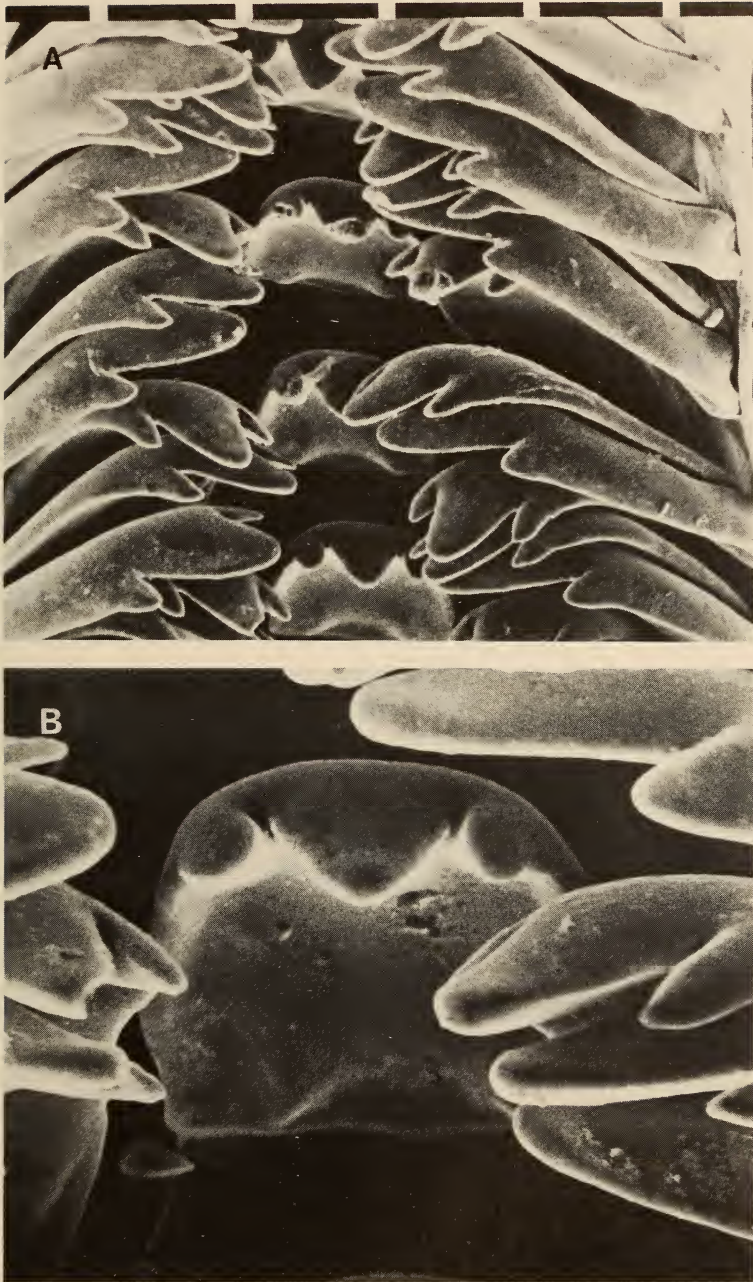


Fig. 22. *Cypraea edentula* Gray, 1825. Scanning electron micrographs of radula.
 A. Entire width. B. Central region.

thinly calcified with a brown or flesh ground-colour. Fulvous spots or blotches cover the dorsal surface. In some specimens, which are known as *C. edentula* var. *alfredensis* Schilder & Schilder, the shell is noticeably more heavily calcified. In these specimens the denticles tend to be more strongly developed on the labrum and the ground-colour of the shell is slate-grey. In all varieties the margins of the shell are white with brown spots. *Cypraea edentula* var. *alfredensis* may prove to represent a distinct species.

Living animal (Fig. 1G)

The foot is short and posteriorly rounded, the siphon is translucent white, strongly recurved and uneven at its tip. The tentacles are lemon-yellow to orange. They are slightly tapered and rounded at their tip. In one specimen the mantle was dark pink stippled with fine black spots. It had sparse whitish wart-like papillae, which were denser on the labral lobe than on the columellar lobe. On the columellar lobe were three large irregular protuberances. The second specimen had a lighter, more transparent mantle covered with dense green tomentose papillae. A few randomly spaced cabbage-like papillae were also present.

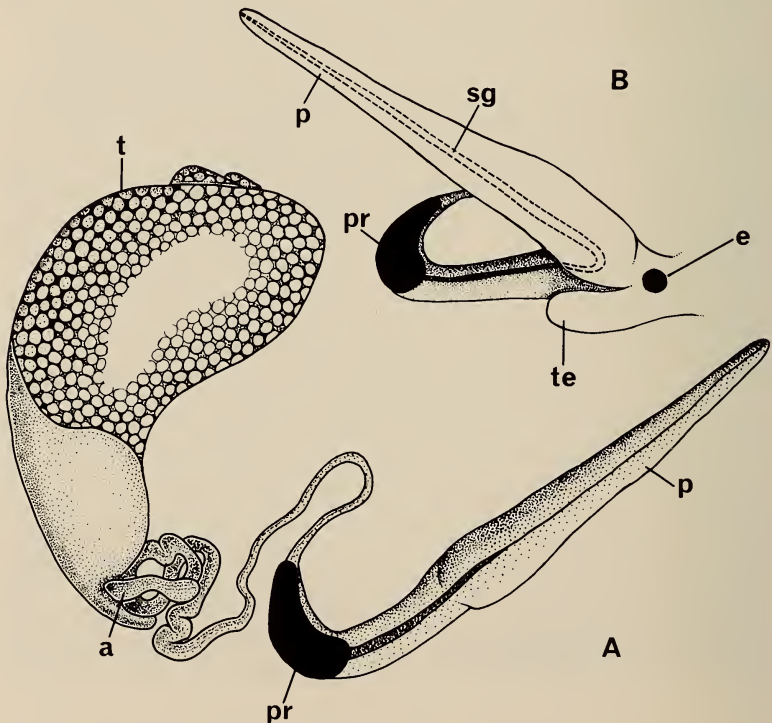


Fig. 23. *Cypraea edentula* Gray, 1825. A. Male reproductive system. B. Penis, opposite view.

Mantle complex

The arrangement of organs is identical to that described for *C. fuscorubra*. The hypobranchial gland is poorly preserved in the present material but the tenidium consists of approximately 150 leaflets. The osphradium is triradiate.

Digestive system

The radular morphology is the only feature of the digestive system that differs from that of *C. fuscorubra*. The radular formula is $66 \times 3.1.3$ in one specimen. The rachidian teeth possess a rounded central cusp with round adjacent cusps (Figs 22, 33F). The base of the rachidian teeth is thin and centrally emarginate. The lateral teeth are broad and possess elongate central and adjacent cusps.

Central nervous system

The arrangement of ganglia is similar to that described for *C. fuscorubra* with a long pleural-subintestinal connective and elongate pedal ganglia.

Reproductive system

Only the male system has been studied (Fig. 23). There is a discrete prostate present at the posterior limit of the sperm groove, as in *C. algoensis*.

Cypraea cruickshanki Kilburn, 1972

Figs 24–27, 33G

Cypraea (Cypraeovula) cruickshanki Kilburn, 1972: 210, pl. 1, text-fig. 1.

Material

A single, freshly dead specimen (SAM-A35987) was collected by a commercial fishing trawler in about 800 m of water approximately 50 km east of Durban. Dead shells of other specimens in the private collections of several individuals were also examined.

Distribution

This species appears to be restricted to the coast of Natal in relatively deep water. It inhabits depths that exceed that of any other known species of *Cypraea*.

Shell (Fig. 24)

The shell is globose, 25.8–33 mm in length. The spire is umbilicate and calloused, covering the protoconch. The labrum is broad, widest centrally and is not glossy. The labrum possesses 20–22 coarse denticles that extend across one-half to three-quarters of the width of the labrum. The anteriormost and posteriormost labral teeth occasionally extend around the labrum, forming tubercles that are visible dorsally. A tubercle is always present on either side of the siphonal canal. The aperture is narrow, widest anteriorly. There are

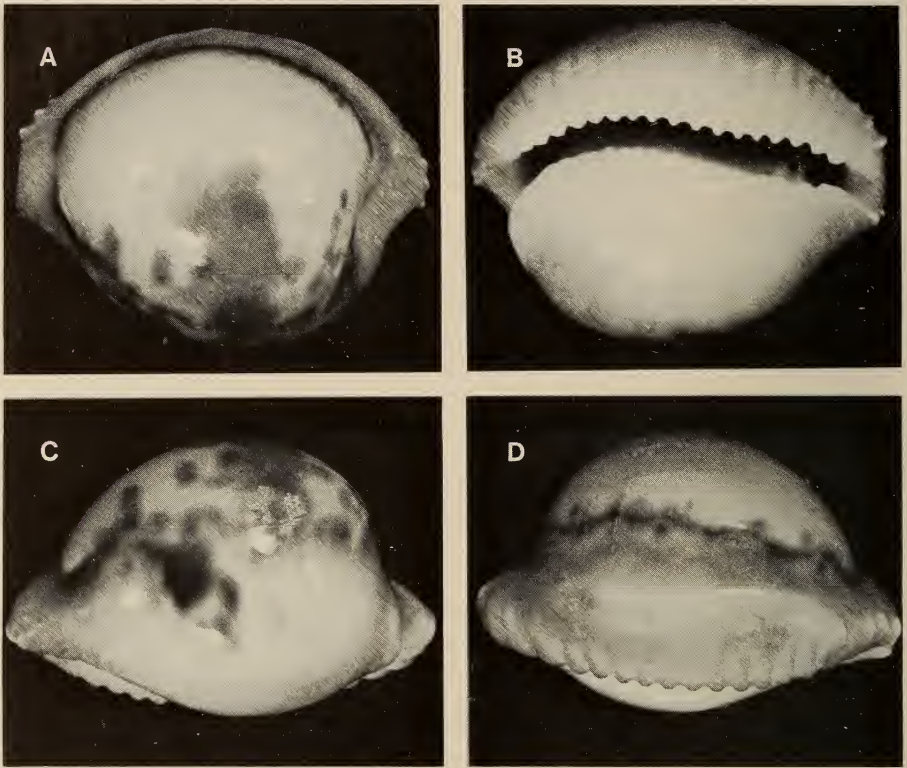


Fig. 24. *Cypraea cruickshanki* Kilburn, 1972. Shell (dorsally pigmented specimen).
 A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect (left). D. Lateral aspect (right).

18–21 columellar teeth, which are finer than the labral teeth. The fossula is well developed with 4–7 weak to strong denticles. The dorsum may be white, yellow or orange. Occasionally specimens may have brown dorsal spots or blotches.

Living animal

Although living specimens have not been observed, the freshly dead specimen examined in this study had a smooth mantle and foot that were whitish in colour. The slender tentacles were also white.

Mantle complex

The organs within the mantle cavity are arranged in the same manner as in *C. fuscorubra*.

Digestive system

The buccal mass, oesophagus, digestive gland and intestine are arranged in the same fashion as in *C. fuscorubra*. The radular formula is $76 \times 3.1.3$ in the single specimen examined. The rachidian tooth (Figs 25, 33G) is broad with a pair

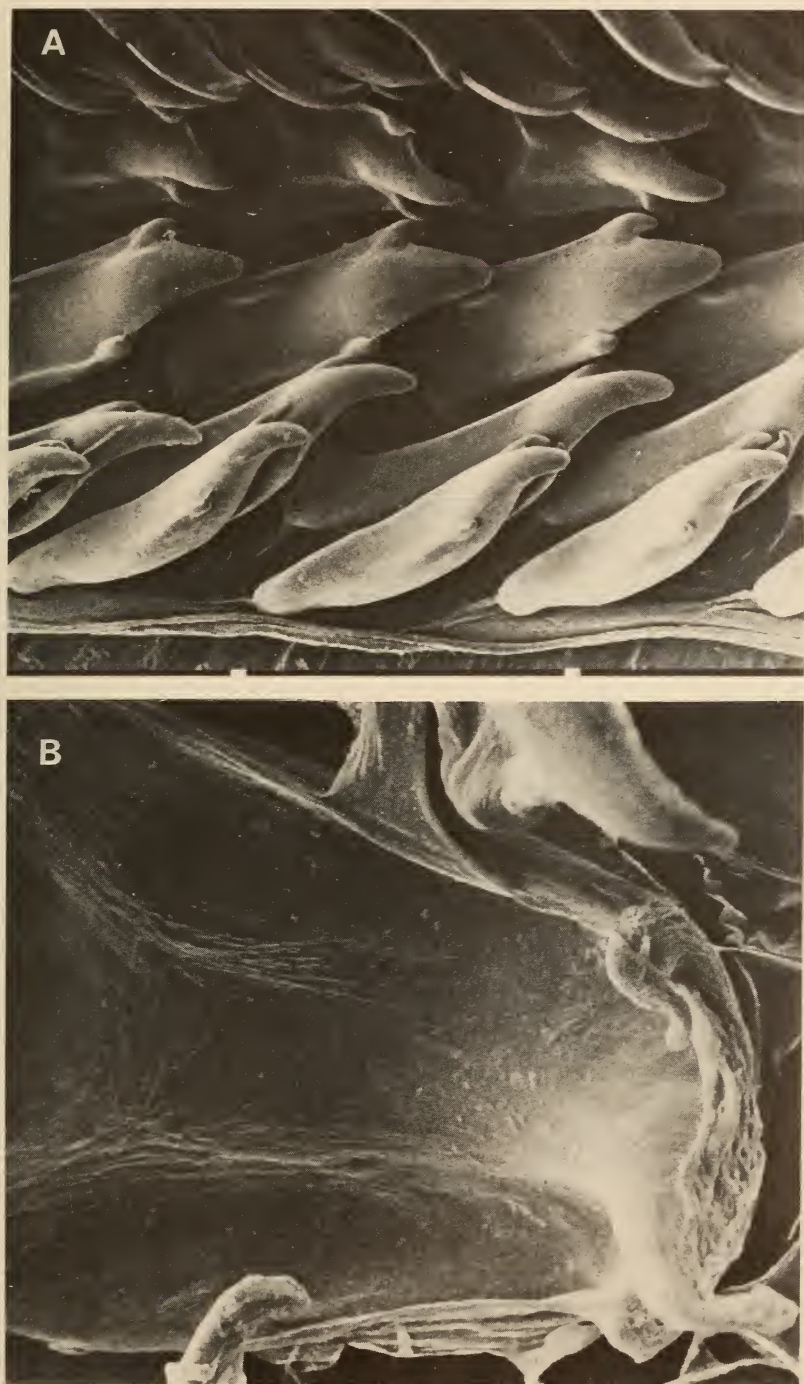


Fig. 25. *Cypraea cruickshanki* Kilburn, 1972. Scanning electron micrographs of radula. A. Entire width. B. Central region.

of ridges on either side of the centre of the tooth. The base of this tooth is well developed and centrally emarginate. On either side of the rounded central cusp is a round denticle. The central cusp and adjacent denticles are rounded on the inner lateral tooth and increase in length successively in the outer two laterals.

Central nervous system

The arrangement of ganglia is similar to that described for *C. fuscobra* with the exception of the pedal ganglia. In *C. cruickshanki* (Fig. 26) the pedal ganglia are spherical with nerves extending from their posterior surface.

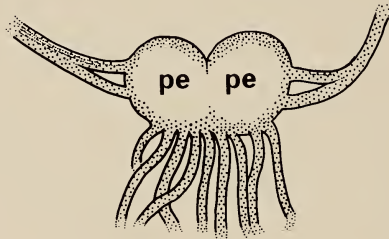


Fig. 26. *Cypraea cruickshanki* Kilburn, 1972.
Pedal ganglia.

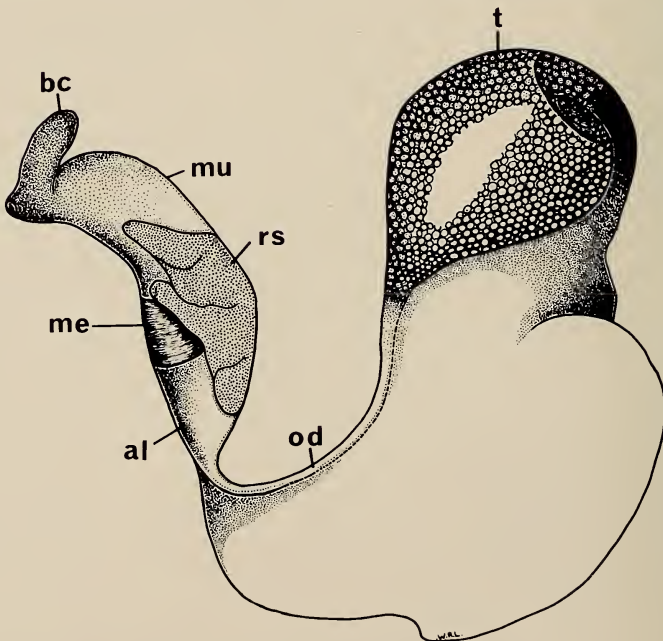


Fig. 27. *Cypraea cruickshanki* Kilburn, 1972. Female reproductive system.

Reproductive system

The single specimen available is a mature female (Fig. 27). The configuration of the reproductive organs is similar to that described for *C. fuscrobura*. However, the glandular receptaculum seminis of *C. cruickshanki* is less ramified than that of *C. fuscrobura*.

Cypraea iutsui (Shikama, 1974)

Figs 28–31, 33H

Cypraeovula (Crossia) iutsui Shikama, 1974: 24, fig. 2.

Material

The single preserved specimen (SAM-A35986), an immature female, was collected by the Department of Zoology of the University of Cape Town in 360–365 m of water off Cape Point.

Distribution

Specimens have been collected from the Olifants River mouth on the Atlantic coast of the Cape Province to the vicinity of Port Elizabeth, on the south-east coast.

Shell (Fig. 28)

The shell is globose, 23 to 38 mm in length. The spire is umbilicate and the protoconch is generally obscured. The labrum is rough in texture and not glossy. Its edge bears 17–25 fine teeth, which are generally white but occasionally are tinged with brown. These teeth extend across about one-quarter of the width of the labrum. The aperture is narrow and curved posteriorly. The columella possesses 12–23 teeth, which are strongest anteriorly. The fossula is poorly developed and generally lacks denticles. In one specimen three weak teeth are present on the fossula. The dorsal surface of the shell is pinkish with dense chestnut mottling. The basal callus is thin and white.

Living animal

The mantle surface is smooth off-white with fine irregular black dots.

Mantle complex

The arrangement of the organs within the mantle cavity is largely the same as in *C. fuscrobura*.

Digestive system

As in the preceding species the digestive system of *C. iutsui* is identical to that found in *C. fuscrobura*, with the exception of the radula. The radular formula is $80 \times 3.1.3$. The rachidian teeth are rectangular with a thickened central area and a strong slightly emarginate base (Figs 29, 33H). Their central cusp is

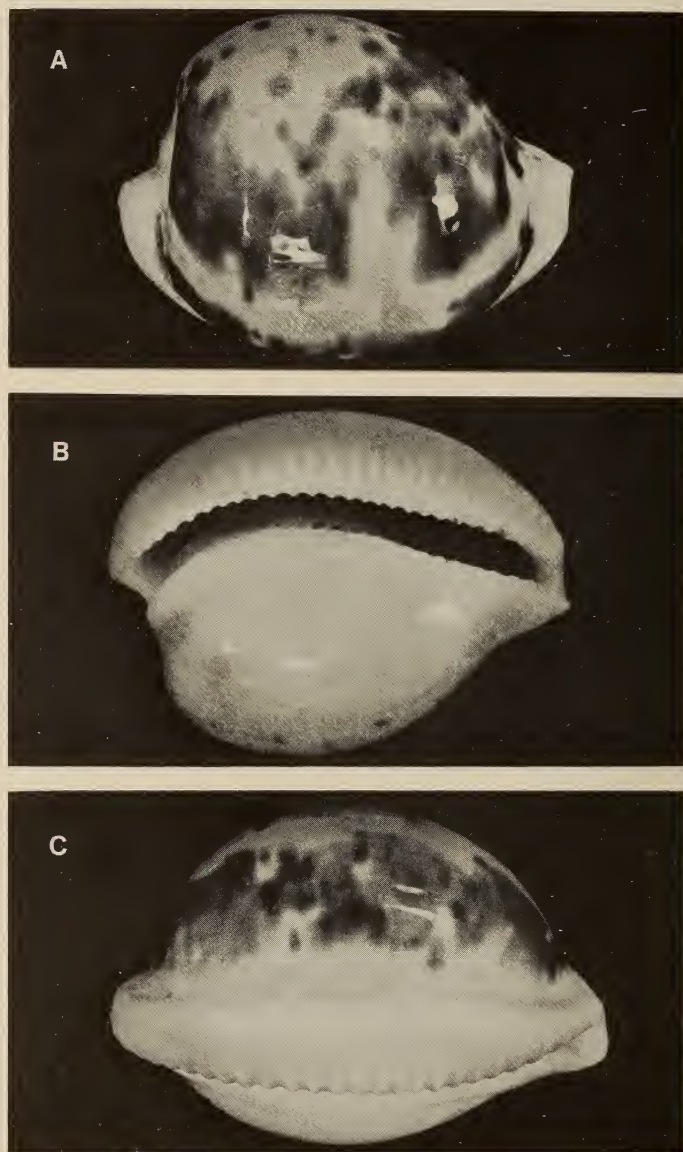


Fig. 28. *Cypraea iutsui* (Shikama, 1974). Shell. A. Dorsal aspect. B. Ventral aspect. C. Lateral aspect.

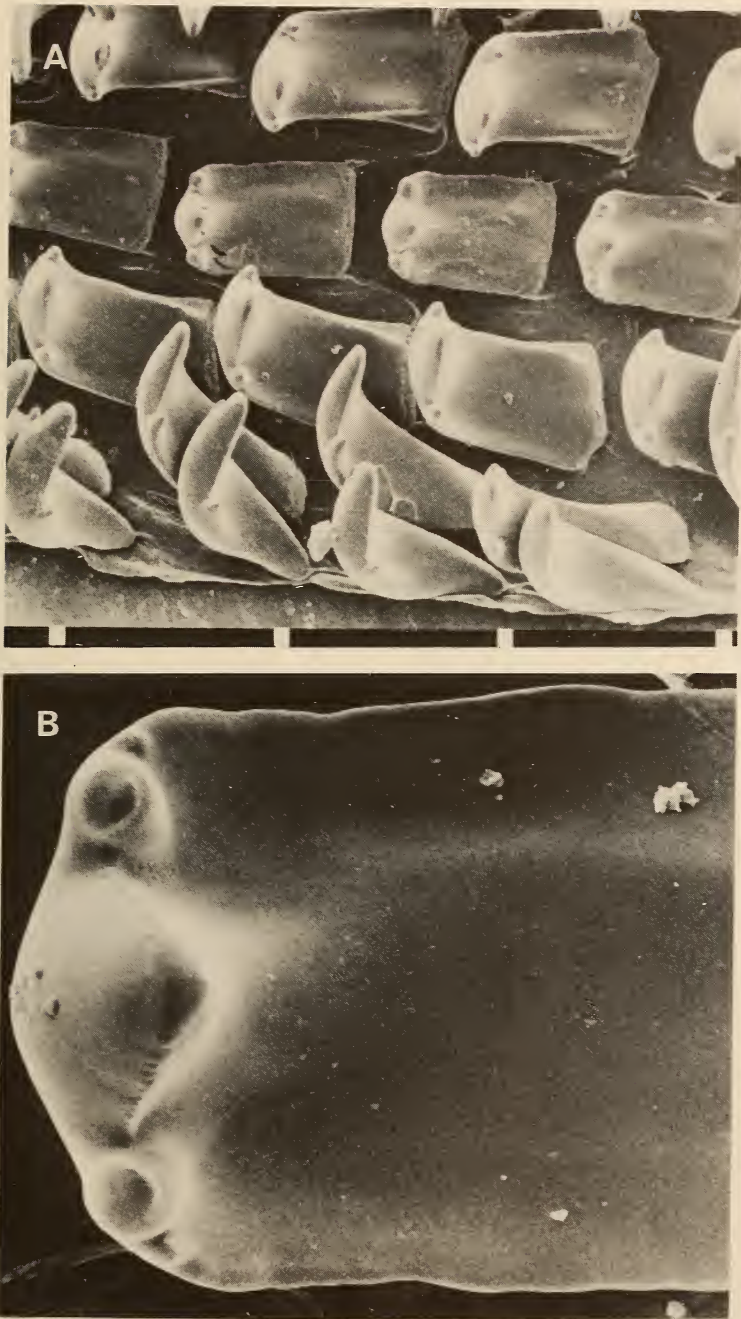


Fig. 29. *Cypraea iutsui* (Shikama, 1974). Scanning electron micrographs of radula. A. Entire width. B. Central region.

rounded, triangular with round lateral denticles. On either side of the lateral denticles is a rounded central cusp, as in *C. coronata*. The lateral denticles, unlike those of *C. coronata*, lack secondary denticles on their inner edge.

Central nervous system

The ganglia of *C. iutsui* differ in their arrangement from that described for *C. fusciorubra*. *Cypraea iutsui* is significantly more cephalized than any other of the South African endemic Cypraeidae. Most notably, the lateral nerve cord has been shortened so that the left pleural ganglion is immediately adjacent to the subintestinal ganglion (Fig. 30). As in *C. cruickshanki*, the pedal ganglia are spherical but there is only a single pair of nerves, which extend from the anterior rather than posterior end of the ganglia.

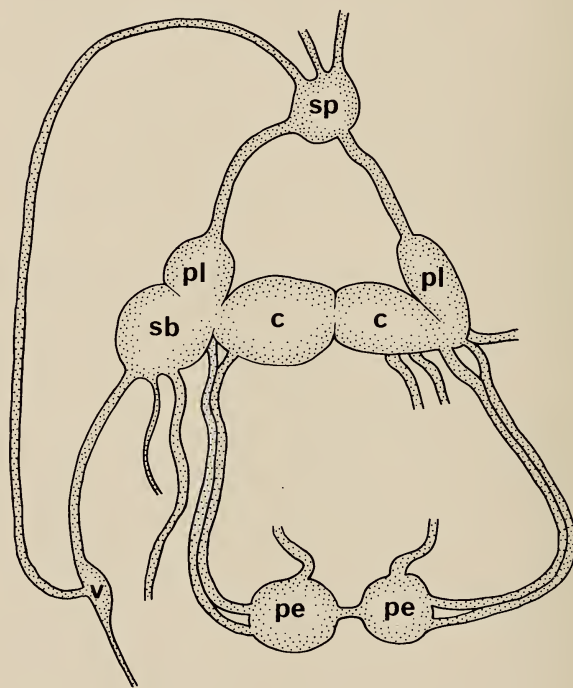


Fig. 30. *Cypraea iutsui* (Shikama, 1974).
Central nervous system.

Reproductive system

The single specimen is an immature female (Fig. 31). The oviduct has not yet undergone differentiation into the female gland mass and receptaculum seminis, although the bursa copulatrix is well developed.



Fig. 31. *Cypraea iutsui* (Shikama, 1974).
Immature female reproductive system.

BIOLOGICAL OBSERVATIONS

Ecology

The majority of known species of cowries are found in shallow tropical seas. Only a few species are known from temperate waters. *Cypraea spadicea* is known from cold waters of central and southern California. Only in southern Australia and South Africa are there large faunas of temperate endemics, consisting of more than ten species.

Eleven of the endemic South African cowries are limited to temperate waters, but four endemic species are restricted to the warm, subtropical waters of Natal.

The endemic cowries of southern Africa are unusual in that they are generally restricted to the sublittoral zone, the only exception being two specimens of *Cypraea capensis* that were found in the intertidal zone at Gonubie, near East London (Kilburn & Aiken 1972). Several species, *C. citrina*, *C. fuscorubra*, *C. fuscodentata*, *C. coronata*, *C. capensis*, *C. edentula* and *C. algoensis* are found in the sublittoral as shallow as 10–100 m depth, while *C. cruickshanki* and *C. iutsui* are known from depths of 400–800 m and 110–365 m, respectively. The depth distributions of *C. lisetae** and *C. fultoni* remain largely unknown as most specimens have been collected from fish stomachs.

Most cowries are known to prey on a variety of benthic algae and invertebrates including sponges, polychaetes and bryozoans, but little is known about their prey specificity. Hayes (1983) has recently demonstrated that the diet of some species of *Cypraea* may be restricted to a single species of sponge while others are far more generalized predators. *Cypraea coronata*, *C. fuscorubra*, *C. fuscodentata* and *C. algoensis* are often found in association with sponges. The intestine of the single specimen of *C. iutsui* examined in this study was full of sponge spicules, as were those of individuals of *C. edentula* and *C. fuscorubra*. *Cypraea coronata* has also been found together with bryozoans and polychaetes. Darkly pigmented specimens of *C. algoensis* from False Bay are usually found upon or adjacent to the crinoid *Comanthus wahlbergi*.

Developmental biology

Those tropical species of Cypraeidae of which the developmental patterns have been described possess a free-swimming veliger stage that metamorphoses

* See note on p. 122.

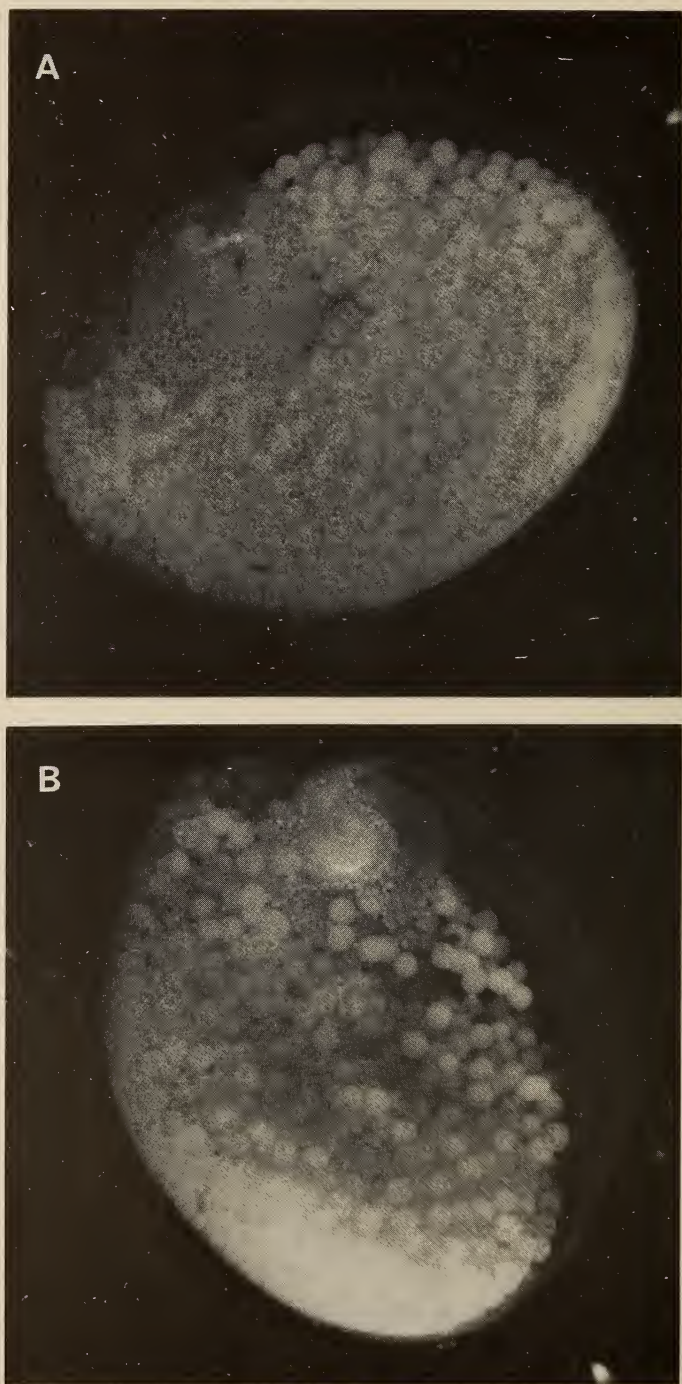


Fig. 32. *Cypraea algoensis* Gray, 1825. A-B. Developing embryos.

into a juvenile following a variable planktonic phase (Ostergaard 1950). Direct development has been observed in several species from southern Australia (Griffiths 1962) and in *Cypraea mus* from the northern coast of South America (Anonymous 1981). Kilburn & Rippey (1982) suggested that the cold-water endemics from southern Africa might exhibit direct development since the temperate Australian species demonstrate this pattern of development. In this study we have observed developing embryos of three species of endemic South African cowries, *C. algoensis*, *C. fuscudentata* and *C. fusciorubra*. These three species lack a free-swimming veliger stage and the post-metamorphic juvenile emerges directly from the egg capsule. The eggs are generally laid on the under-surface of rocks and are brooded by the female. One egg mass of *C. fuscudentata* consisted of 52 capsules with numerous white eggs. The capsules are 3.9 mm in diameter. The egg mass of *C. algoensis* consisted of 28 egg capsules, 3.8–4.0 mm in diameter, and contained whitish or yellow eggs. A single egg capsule was laid in a bucket of sea water by a freshly collected specimen of *C. fusciorubra*. It was similar in size and appearance to the capsules of the other two species. Developing embryos have been observed only in *C. algoensis*. The velum is greatly reduced but recognizable as a single ovoid lobe (Fig. 32). Juveniles have not been observed hatching from the egg capsules but well-developed embryos (Fig. 1H) have been observed with nurse eggs and were probably about ready to emerge from the egg capsules.

MORPHOLOGY OF *PEDICULARIA CALIFORNICA* NEWCOMB, 1864

Examination of specimens of *Pedicularia californica* Newcomb, 1864, in the course of this study, yields several interesting facts. The osphradium is triradiate with leaflets absent from the left margin (Fig. 34A). The pedal ganglia are spherical in shape without posteriorly directed extensions. The animals are gonochoric. The male system (Fig. 34B) consists of a highly convoluted ampulla, which gradually forms a short vas deferens. The tubular vas deferens terminates near the opening of the mantle cavity, where it empties into a ciliated sperm groove. The sperm groove continues along the right side of the body and along the ventral side of the penis. Kay (1957a) erroneously stated that *Pedicularia* has closed reproductive ducts. At the base of the penis is a dermal prostate gland that empties into its own ciliated groove and joins the sperm groove. The female system (Fig. 34C) is similar to that described by Ghiselin & Wilson (1966) for *Cyphoma gibbosum*, except that an ectal bursa copulatrix is absent.

GENERIC SUBDIVISION

The Cypraeidae represent a large family of gastropods with an extensive literature, primarily owing to their interest to shell collectors. Most of these works are strictly conchological or distributional in nature and few morphological



Fig. 33. Radulae of South African Cypraeidae. A. *Cypraea fuscorubra* Shaw, 1909. B. *Cypraea algoensis* Gray, 1825. C. *Cypraea coronata* (Schilder, 1930). D. *Cypraea fuscodentata* Gray, 1825.

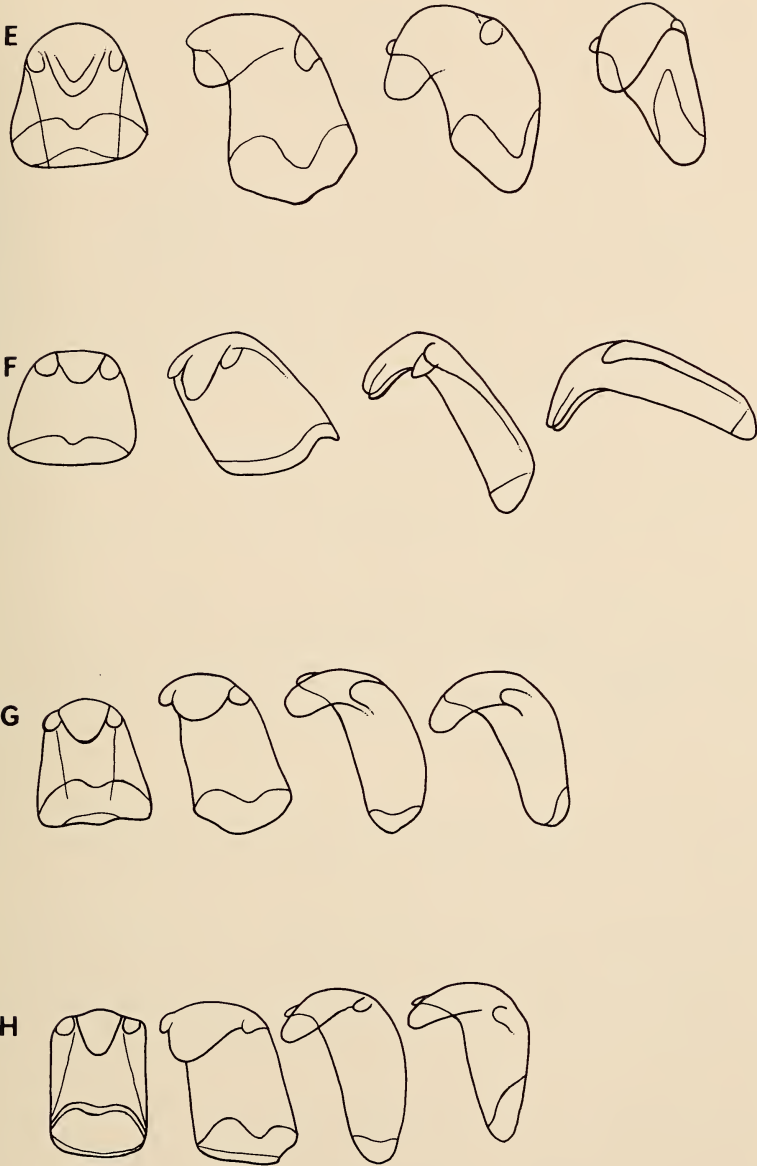


Fig. 33 (continued). E. *Cypraea capensis* Gray, 1828. F. *Cypraea edentula* Gray, 1825.
 G. *Cypraea cruickshanki* Kilburn, 1972. H. *Cypraea iusui* (Shikama, 1974).

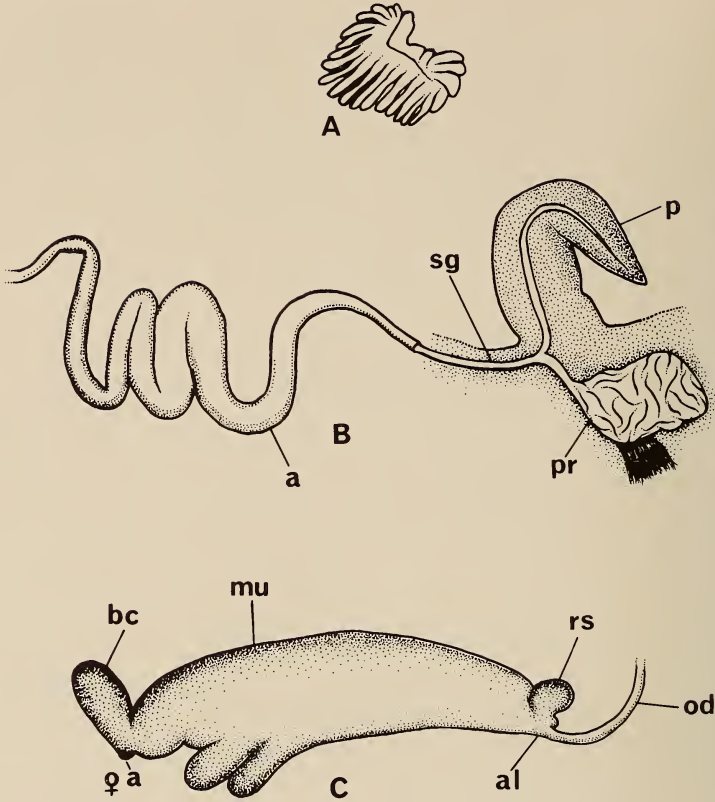


Fig. 34. *Pedicularia californica* Newcomb, 1864. A. Osphradium. B. Male reproductive system. C. Female reproductive system.

studies have been conducted (Shaw 1909; Vayssière 1923, 1927; Riese 1931; Rau 1934; Risbec 1937; Kay 1960a, 1960b, 1961, 1963). Wilson & McComb (1967) utilized subgeneric names within *Cypraea*. Kay (1960a: 283) stated that 'the species of *Cypraea* thus far examined are characterized by an extremely conservative anatomical picture'. However, she described considerable variability in the radula and female reproductive morphology, which had not previously been recorded. Recognition of these features resulted in species groups that differed from previous systems, which were based largely on conchological features. As the morphology of about only one-third of the described species was known, Kay (1960a) stated that it was better to include all members of the Cypraeidae in the single genus *Cypraea* until more comparative data became available. This was a dramatic departure from previous classifications (Schilder 1936; Steadman & Cotton 1946; Allan 1956), which subdivided the family into 24–61 genera. Subsequently, Cernohorsky (1965) incorporated many of the specific changes suggested by Kay (1960a), but divided the family into 28 genera.

A similar situation exists in the closely allied Triviidae. Cate (1979) subdivided the triviids into 15 genera based solely on conchological features. More recently, Gosliner & Liltved (1982) found considerable variation in internal morphology and suggested that all species be contained in the single genus *Trivia* until sufficient information was available to ascertain natural groupings. The fact that the present study demonstrates even greater morphological variability within the Cypraeidae supports Kay's contention that insufficient information is presently available to divide the family. The present study therefore maintains all species within the single genus *Cypraea*, until the morphology of the endemic Cypraeidae of southern Africa is more fully known.

MORPHOLOGICAL VARIABILITY

Great variability exists in the morphology of the shell. Despite claims by several workers that there is little morphological variability in the Cypraeidae, most organ systems vary considerably more than previously indicated. For this reason it is imperative to review the available morphological data.

Shell

The South African endemic cypraeids exhibit a propensity for sinistrality not found in other members of the family. Sinistral shells are rare, in any case, but have been found in specimens of *Cypraea edentula*, *C. fuscodentata* and *C. capensis*.

Mantle

Schilder (1936), Kay (1963), Cernohorsky (1965), and Wilson & McComb (1967) have suggested that the coloration and ornamentation of the mantle and siphon in living specimens are important criteria for distinguishing species. This is particularly true of the shape of the papillae. Schilder (1936) stated that closely allied species such as *C. staphylea* and *C. limacina* can be distinguished by their shells and living animals despite the fact that their radulae are very similar. The usefulness of mantle characteristics for the separation of species groups into higher taxa has been successfully employed (Kay 1963, 1981) but needs to be more fully explored.

Our observations of living representatives of these species from South Africa in the present study confirm Schilder's (1936) observations. Within the endemic South African Cypraeidae most species possess simple wart-like papillae. In *C. algoensis*, *C. fuscodentata* and *C. fuscorubra* the number and density of papillae are variable and they may often be entirely absent. The mantle of *C. coronata*, on the other hand, is always densely papillate with wart-like tubercles. In *C. edentula* cabbage-like papillae are present in addition to simple ones. The colour of the mantle varies intraspecifically. *Cypraea fuscorubra* exhibits the greatest variability in coloration while in *C. coronata* only the proportions of the various pigments vary. Despite the intraspecific variability of mantle colour most

South African endemic species can be distinguished on the basis of their mantle characteristics (Fig. 1).

Mantle complex

A certain degree of variability has been described for the mantle complex in the Cypraeidae. Schilder (1936) suggested that differences in elaboration of the osphradium and ctenidium might constitute a basis for the division of genera in the family. Kay (1960a) stated that such differences might be useful in separating closely related species but discounted their usefulness in separating genera. Later (1963) she noted that *C. testudinaria* and *C. hesitata* are unique in having a bifid rather than triradiate osphradium, but all other morphological features confirm that the species are not closely related. From this study it is apparent that there is little variation in the morphology of the mantle complex between species of endemic South African cypraeids.

Digestive system

The morphology of the digestive system of *Cypraea* has been studied by Rau (1934), Risbec (1937), and Kay (1960b). Minor interspecific differences have been noted in the elaboration of the salivary glands, stomach and buccal mass (Risbec 1937) but their intraspecific variability has not been fully determined. Therefore the systematic value of these characters remains open to question.

There is little variation in the gross morphology of the digestive system in the species examined in this study, and the pattern agrees with that described by Rau (1934, fig. 43) and Kay (1960b) with the exception that the salivary glands are largely fused into a single mass.

Most of the variation in the digestive system has been focused on the morphology of the radular teeth. Kay (1960a) described four basic radular types. The majority of species are known to possess a 'R1' radula with dumb-bell shaped internal bracts at the base of the rectangular rachidian tooth. Within this radular 'type' there seem to be several major variants. The presence or absence of basal denticles on the rachidian and inner lateral teeth and the subtending bract at the base of the rachidian appear to be species-specific. Kilburn & Aiken (1972) noted that the radula of *C. fultoni* lacked a subtending bract and denticles and compared its radula to that of *C. rosselli* (Wilson & McComb 1967). The same morphological pattern is found in the radulae of all of the other South African endemics examined in this study. No species studied had either subtending bracts or basal denticles. The radular teeth of *C. edentula* and *C. algoensis* appear to be significantly broader than those of any cypraeids with a 'R1' radula and differ markedly from those of other South African species (Fig. 33). Kay (1960a) stated that in *Cypraea* the radular teeth generally possess a single denticle on either side of the central cusp. Kilburn & Aiken (1972) noted that in the specimen of *C. fultoni* that they examined, there is a smaller secondary denticle on the outer side of the primary cusp and questioned whether this is characteristic of the species. Secondary denticles have also been described in several other species (Vayssière

1923, 1927; Risbec 1934). In the single specimen of *C. iutsui* examined in this study, secondary denticles are present on the rachidian tooth although they were not indicated by Barnard (1963, fig. 5C, as *C. fuscorubra* 'globose form'). Secondary denticles on the rachidian teeth and on the inner side of the inner laterals are characteristic of all specimens of *C. coronata* examined in this study (Fig. 13B).

A great deal more information is required to determine the range of variability within and between species of *Cypraea* to ascertain the systematic significance of the observed radular differences.

Central nervous system

The central nervous system in the Cypraeidae is highly modified from that of less specialized mesogastropods such as *Littorina* (Fretter & Graham 1962). The lateral nerve cords do not cross each other and are largely euthyneurous. A short zygoneurous connective links the left pleural and supraintestinal ganglia. There does not appear to be a zygoneurous connection between the right pleural ganglion and the subintestinal ganglion, although a thin connective was indicated by Riese (1931).

Shaw (1909) differentiated *Trivia* from *Cypraea* on the basis of the shape of the pedal ganglia: elongate in *Cypraea* and spherical in *Trivia*. This has served as a major criterion for separating the Cypraeacea from the Lamellariacea (Schilder 1936). Since Shaw's (1909) work all three subsequent studies of the nervous system of the Cypraeidae (Riese 1931; Risbec 1937; Kay 1957*b*) have confirmed the presence of elongate pedal ganglia within the family. Specimens of *C. fuscorubra*, *C. fuscodentata*, *C. coronata*, *C. algoensis*, *C. edentula* and *C. capensis* examined in this study had elongate pedal ganglia (Fig. 7). However, the ganglia of *C. iutsui* and *C. cruickshanki* are spherical as described for the Lamellariacea. In *C. cruickshanki* there are several elongate nerves emanating from the posterior ends of the ganglia (Fig. 26), while in *C. iutsui* a single pair of nerves extends anteriorly (Fig. 30).

Most authorities have stated that there is very little variability within the nervous system in the Cypraeidae. In addition to the differences already noted in the pedal ganglia, the length of the lateral nerve cord between the left pleural and subintestinal ganglia varies considerably between species. Risbec (1937) demonstrated that in species from New Caledonia this nerve cord is elongate in *C. arabica*, *C. lynx*, *C. tigris* and *C. carneola*, and short in *C. clandestina*, *C. moneta*, *C. annulus* and *C. erosa*. In *C. staphylea* the subintestinal ganglion is immediately adjacent to the left pleural ganglion. In all of the South African cowries examined in this study the lateral cord is elongate, with the exception of *C. iutsui*, in which the pleural and subintestinal are adjacent as in *C. staphylea*.

Risbec (1937) also noted that a variable number of accessory ganglia are present along the lateral nerve cords in the various *Cypraea* species he studied. Some species, such as *C. clandestina*, have only a single accessory ganglion. *Cypraea erosa*, *C. moneta*, *C. erroneus* and *C. annulus* possess two ganglia;

C. staphylea and *C. carneola* three, *C. arabica* four, and *C. tigris* seven. All the South African species examined have only a single accessory ganglion present between the suprainstestinal and visceral ganglia, as in *C. staphylea*.

Reproductive system

Kay (1960a) described two basic forms of the female reproductive system of the Cypraeidae: in the first instance a bursa copulatrix is present and also a glandular receptaculum seminis, which is granular in texture; in the second form a bursa is absent but a saccate receptaculum is present. Kay (1963) described interspecific morphological variability in the shape of the bursa copulatrix. Kilburn & Aiken (1972) stated that in the reproductive system of *C. capensis* a bursa is present and the receptaculum is apparently glandular. All of the six species of South African Cypraeidae in which the female reproductive system was examined in this study, possess a bursa copulatrix and a saccate, diverticulate receptaculum seminis. In each instance the bursa is simply saccate as described from *C. argus* (Kay 1963, fig. 6a). The receptaculum, although saccate, appears to have a glandular epithelium, but this needs to be verified by means of histological examination. The fact that all South African endemic species thus far examined (with the possible exception of *C. capensis*, which needs to be re-examined) possess both a saccate receptaculum and a bursa further suggests that the structure of the female reproductive system is likely to be systematically significant.

Little variation has been described in the male system of the Cypraeidae. There appear to be only minor differences in the shape of the penis (Kay 1960a). All of the South African species examined possess a simple conical penis with a ventral sperm groove extending to its tip as described by Kay (1960b). The prostate in *Cypraea* has been described as an elongate, club-shaped or rectangular structure (Kay 1960a). Wilson & McComb (1967) described some variation in the shape and size of the prostate. In the South African Cypraeidae there are two types of prostate glands. In *C. fuscudentata*, *C. fuscocorubra* and *C. coronata* a distinct prostate is absent and the walls of the sperm groove are lined with glandular cells (Fig. 8B). In *C. edentula* and *C. algoensis* a discrete prostatic region is situated at the ental end of the sperm groove (Figs 11B, 23).

SYSTEMATICS OF ENDEMIC SOUTH AFRICAN CYPRAEIDAE

The taxonomy of the endemic Cypraeidae of southern Africa has historically been a source of considerable confusion, and this situation persists. The precise number of constituent taxa cannot be accurately determined at present. Until now the majority of species have been known only from beach-worn shells. While many questions remain unanswered, the information presented in this study does permit some of the systematic controversy to be resolved.

The endemic Cypraeidae of South Africa consist of several major components. *Cypraea citrina* Gray, 1825, is found from the coast of Mozambique

to Jeffreys Bay in the eastern Cape Province. It appears to be closely allied to the widespread Indo-Pacific species *C. helvola* and *C. marginalis*, although nothing is known about its internal morphology. *Cypraea lisetae* Kilburn, 1975,* is conchologically most similar to *C. midwayensis*, which was designated as the type species of *Nesiocypraea* Azuma & Kurohara, 1967, because of the unique shape of the rachidian teeth. Unfortunately the radula of *C. lisetae* remains unknown. *Cypraea fultoni* Sowerby, 1903, has been placed in *Bernaya* and appears to be allied to several species that are restricted to south-western Australia (Schilder 1936).

The remaining endemic species have been placed in the genera *Luponia* and *Cypraeovula* (Schilder 1936), which appear to be restricted to southern Africa but may be allied to the south-western Australian endemics. Within these taxa there appear to be three species complexes, which can be recognized conchologically and by their internal morphology. The first group consists of *Cypraea cruickshanki* Kilburn, 1972, and *C. iutsui* (Shikama, 1974). The status of these species has been the subject of much debate. When Kilburn described *C. cruickshanki* he also included photographs and a discussion of several specimens that Barnard (1963) had previously considered as a globose form of *C. fuscrobura* Shaw. Kilburn contended that this form appeared to be distinct from *C. fuscrobura* and was similar to *C. cruickshanki*, but insufficient material prevented a detailed comparison. Shikama (1974) described *Cypraeovula iutsui* based on a single specimen collected from southern Africa. Burgess (1977) suggested that *Cypraea iutsui* is merely the fully mature stage of *C. cruickshanki*. Kilburn & Rippey (1982) recently stated that *C. iutsui* is either a cold-water form of *C. cruickshanki* or a deep-water form of *C. fuscrobura*. Examination of preserved animals and shells in this study confirms that *C. iutsui* is distinct from both *C. cruickshanki* and *C. fuscrobura*. The conchological features distinguishing *C. iutsui* (as *C. fuscrobura* globose form) from *C. cruickshanki* described by Kilburn (1972: 214, table II) are consistent with material examined in this study. The most obvious difference between the two is the prominent versus fine labral teeth of *C. cruickshanki*, which traverse most of the width of the labrum. The fossula of *C. cruickshanki* is prominent with 4–6 denticles while in *C. iutsui* it is poorly developed with no or, more rarely, three denticles. In *C. iutsui* the posterior limit of the labrum extends beyond the body whorl while in *C. cruickshanki* they are approximately the same length. In *C. cruickshanki* the anterior and posterior columellar teeth extend on to the columella while in *C. iutsui* they do not.

The internal differences between the two species are even more profound. The rachidian teeth of *C. cruickshanki* have a narrow raised portion while in *C. iutsui* this area is much wider (Figs 29, 33). *Cypraea iutsui* has small accessory denticles on the outer side of the rachidian tooth, which are absent in *C. cruickshanki*. The most significant morphological differences are present in the central nervous system. In *C. iutsui* the subintestinal ganglion is immediately

* See note on p. 122.

adjacent to the left pleural ganglion while in *C. cruickshanki* they are separated by a moderately long nerve cord. The nerves emanating from the pedal ganglia are anteriorly directed in *C. iutsui* and posteriorly directed in *C. cruickshanki*. The two species appear to be entirely geographically isolated, as well.

Burgess (1977) suggested that *C. cruickshanki* should probably be placed in a separate genus based on its conchological uniqueness. The fact that *C. cruickshanki* and *C. iutsui* are the only cypraeids known to possess spherical pedal ganglia adds credence to this idea. However, more information concerning the range of variability of this character within the Cypraeidae is required to establish generic or subgeneric limits.

The second major group of endemic cypraeids includes *Cypraea algoensis* Gray, 1825, and *C. edentula* Gray, 1825. Conchologically these two species are pyriform to globular. In both cases the margin of the shell is ornamented with dark purple or brown spots. These taxa share certain internal features that are absent from other South African cypraeids. The radular teeth are significantly broader than in other species and a discrete prostate gland is present. These characteristics may justify the placement of these taxa within the distinct subgenus *Luponia* Broderip, 1837. *Cypraea edentula* and *C. algoensis* can be distinguished by several conchological and morphological features. *Cypraea edentula* generally lacks labral or columellar teeth, but rudiments may occasionally appear on the labrum. *Cypraea algoensis* possesses fine but well-developed teeth on the labrum and columella. In *C. edentula* the fossula is well developed and strongly denticulate while it is poorly developed with occasional denticles in *C. algoensis*. There appear to be slight but consistent radular differences between the two species. The central and adjacent cusps of the rachidian teeth are rounded in *C. edentula* and elongate in *C. algoensis*. There do not appear to be any significant differences in the nervous and reproductive systems. The two species are geographically isolated; *C. edentula* is known from Tsitsikama Coastal National Park to the south-western Transkei, while *C. algoensis* has been found from the Atlantic coast of the Cape Peninsula to Cape Agulhas.

The largest number of endemics are contained within the third group. The constituent species of this group have been the subject of considerable systematic confusion and disagreement. Unfortunately the morphology of several of these taxa remains largely unknown. All authorities who have studied the South African Cypraeidae agree that *Cypraea fuscudentata* Gray, 1825, *C. fuscrobura* Shaw, 1909, and *C. capensis* Gray, 1828, represent distinct valid species. Beyond this, there is little agreement about the systematics of the remaining taxa.

Much of the controversy surrounding this group relates to a pair of species that have been confused, synonymized, or renamed owing to homonymy. A detailed historical account of the problems is provided by Burgess (1982). Briefly, *Cypraea similis* Gray, 1831, was found to be a junior homonym of *C. similis* Gmelin, 1791 (= *C. erosa* Linnaeus, 1758). Later, *Cypraea castanea* Higgins, 1868, was discovered to be a junior homonym of *C. castanea* Röding, 1798. Shaw (1909) noted this problem and considered Gray's and Higgins' species as

subjective synonyms. He provided *C. fuscorubra* as a new name for *Cypraea similis* Gray and designated Gray's specimen as the holotype of *C. fuscorubra*. Burgess (1970) recognized that there were conchological differences distinguishing Gray's and Higgins' material but erroneously provided a new name for Gray's rather than Higgins' material. Thus *C. gondwanalandensis* became a junior objective synonym of *C. fuscorubra* Shaw (Kilburn 1972). This error was corrected by Burgess (1982): he named *C. verhoefi* based on Higgins' holotype of *C. castanea*. Kilburn & Rippey (1982) considered *C. verhoefi* (as *C. castanea*) as a junior subjective synonym of *C. fuscorubra* despite the significant conchological differences discussed by Burgess (1970, 1982). No preserved animals of *C. verhoefi* have been examined, nor are any presently available. A definitive statement concerning the taxonomic status cannot be made until the morphology of *C. verhoefi* is known, but the consistent conchological differences between them strongly suggest that Burgess is correct in maintaining their separation.

Cypraea coronata (Schilder, 1930), which is normally characterized by having tubercles around the outer margin of the shell, has not been reported in the literature since its original description. Kilburn & Rippey (1982: 62) considered it as an 'interesting form of *C. fuscudentata*'. There are several conchological characters separating *C. fuscudentata* and *C. coronata*. The presence of tubercles and the slightly irregular outline of *C. coronata* most clearly distinguish it from *C. fuscudentata*. The columellar teeth of *C. fuscudentata* are dark brown and the majority cover most of the width of the columella. In *C. coronata* the teeth are white or light brown and normally only the anteriormost and posteriormost teeth extend beyond the aperture on to the columella. The form of the radular teeth also clearly differentiates the two. *Cypraea coronata* has accessory denticles on the outer edges of the rachidian and inner lateral teeth, which are absent in *C. fuscudentata*. These differences in conchology, internal morphology and appearance of the living animal (Fig. 1) distinguish *C. coronata* as a distinct species.

Cypraea gloriosa (Shikama, 1971) was originally thought to have been collected from the South China Sea. Burgess (1977) and Kilburn & Rippey (1982) have pointed out that it is likely that it was collected off South Africa and consider it synonymous with previously described South African species. However, Burgess considered *C. gloriosa* as a junior synonym of *C. fuscudentata* while Kilburn & Rippey regarded it as a junior synonym of *C. fuscorubra*. The strong dentition of the columellar teeth extending on to the columella is more similar to that found in *C. fuscudentata*. However, the mottled coloration and large tubercles on the margins of the shell indicate that it should be regarded as a junior synonym of *C. coronata*.

The existence of two other taxa has recently been explained as the product of hybridization of well-defined species (Kilburn & Rippey 1982). *Cypraea cohenae* Burgess, 1965, is conchologically intermediate between *C. edentula* and *C. fuscudentata* while *C. amphitales* Melvill, 1888, is similar to *C. capensis* and *C. fuscudentata*. While the conchological intermediacy of these taxa could possibly be explained by hybridization there are no internal morphological or

biological data to support this claim. Detailed observation and examination of living and preserved specimens are required before definitive conclusions can be drawn. The fact that shells of *C. cohenae* are rare and are known only from a very limited geographical area (Jeffreys Bay) does not preclude that they may be relatively common and widespread in the sublittoral. Shells of several cypraeids are rarely found on the beaches of the Cape Peninsula but are fairly commonly found in the shallow sublittoral. If indeed *C. edentula* does interbreed with *C. capensis* and *C. fuscodentata* it would certainly reduce the systematic importance of the radular and prostatic differences between representatives of these species groups.

HIGHER SYSTEMATICS AND PHYLOGENY OF THE CYPRAEACEA AND LAMELLARIACEA

The higher systematics of the Cypraeacea and Lamellariacea within the Mesogastropoda has been the subject of considerable disagreement and confusion. In some cases even the same author has produced several conflicting schemes of classification (Schilder 1936, 1966, 1969).

Much of the argument concerning the classification of these two superfamilies relates directly to the position of the Triviidae (including Eratoinae). Conchologically most triviids appear to be closely allied to the Cypraeidae and Ovulidae and have traditionally been classified with them (Shaw 1909). The discovery of the fact that the Triviidae and Lamellariidae possess a double-shelled larva called an echinospira led Schilder (1936) to suggest that the Triviidae are more closely allied to the Lamellariidae than to the Cypraeidae and Ovulidae. The observation that an echinospira larva is also present in *Capulus ungaricus* (Lebour 1937) further complicated the problem, as the capulids have been considered to be closely allied to the Calyptraeidae and Trichotropidae. On the bases of conchological and larval features Fretter & Graham (1962) stated that the Cypraeacea, Lamellariacea and Calyptraea are all closely allied, and maintained the placement of the Triviidae in the Lamellariacea. More recently, Schilder (1966) altered his opinion and suggested that the Triviidae are more closely related to the Cypraeacea, as did Kay (1960*b*). Speculation with regard to these mesogastropods has significantly exceeded the collection and careful analysis of data. In some cases the examination of one or two species has been employed to characterize an entire family. This has led to erroneous assumptions about morphological variability and its systematic significance. For example, it has been assumed since the work of Shaw (1909) that the Triviidae and Cypraeidae can be separated by the shape of the pedal ganglia. This is shown here to be incorrect as both configurations have been found in the South African Cypraeidae. The degree of morphological variability observed in the Cypraeidae in the present study and previously in the Triviidae (Gosliner & Liltved 1982) attests to the need for the accumulation of more detailed morphological data.

Another major problem in determining phylogeny is the establishment of the direction of evolutionary change. Kay (1960*b*) described differences of opinion as

to whether the elongate pedal ganglia found in most Cypraeidae are primitive or advanced features. None of the arguments put forth as to the ancestral state of the ganglia consider that more primitive mesogastropods such as *Viviparus* possess elongate pedal ganglia, and all ignore the fact that cephalization, or the concentration of nervous tissue into the cephalic region, is one of the most widespread evolutionary trends in the animal kingdom.

Consideration of the distribution of characters within other taxa and their functional significance generally permits one to make a reasonable estimate of the polarity of most characters. The trend to modify an open ciliated sperm groove to a closed tubular vas deferens is widespread throughout the Gastropoda (Kay 1960*b*). Ghiselin (1966) described the functional adaptive significance of this modification in opisthobranchs, while Morton (1955) and Fretter & Graham (1962) have demonstrated the same trend in pulmonates and neogastropods. Gosliner (1981) indicated that the most primitive living mesogastropods are probably littorinaceans and that they possess a sperm groove.

Ghiselin (1966) stated that the most primitive opisthobranchs probably had an ental receptaculum seminis and an ectal bursa copulatrix. This also appears to be the ancestral (plesiomorphic) state of the Pulmonata, Mesogastropoda (Gosliner 1981; Ghiselin & Wilson 1966) and Neogastropoda (Fretter & Graham 1962).

The larval stage of the vast majority of gastropods is a simple veliger. The presence of an echinospira larva in the Triviidae, Lamellariidae and Capulidae most likely represents a secondary modification of the veliger to facilitate flotation in taxa with a prolonged larval life (Fretter & Graham 1962). The question that remains is whether the presence of an echinospira in the Capulidae represents an independent acquisition of this larval type or implies phyletic proximity to the lamellariids and triviids. Adequate morphological information is not presently available to compare the Capulidae with the other taxa.

The osphradium is the primary chemosensory organ in the majority of prosobranch gastropods. In most mesogastropods it is a simple linear structure, but in the Triviidae, Lamellariidae, Naticidae and Neogastropoda it is foliate and bipectinate. This is usually correlated with the development of the siphon and increased predatory capabilities. In the Cypraeidae and Oculinidae, which also possess a siphon, the osphradium is well developed, but is triangular in shape (except where it is secondarily modified in *Cypraea hesitata* and *C. testudinaria* (Kay 1963)). Both the bipectinate and triangular osphradia of these taxa appear to be derived (apomorphic) from a simple linear ridge.

The most primitive mesogastropods such as *Littorina* are generalized grazing omnivores. Many members of the Cypraeidae appear to adopt this mode of feeding (Kay 1960*b*) but others are specialized carnivores (Hayes 1983). The majority of oculinids are specialized predators on alcyonaceans, except for *Pedicularia*, which feeds exclusively on stylasterine hydrozoan corals. The Triviidae and Lamellariidae feed upon, and lay their eggs within, tunicate colonies (Fretter & Graham 1962).

The determination of phylogenetic relationships of taxa may only be based upon shared derived characters (synapomorphies) (Hennig 1966). A comparison of the apomorphies present in the Triviidae, Lamellariidae, Ovulidae and Cypraeidae yields a clear picture of dichotomy between the Cypraeacea and Lamellariacea (Table 1, Fig. 35). The possession of a closed sperm groove, echinospira larva and large bipectinate osphradium unite the Triviidae and Lamellariidae. The morphological synapomorphies shared by the Lamellariidae and Triviidae are largely independent of their ecological association with compound tunicates, reducing the possibility that these similarities are due to parallelism. A triangular osphradium appears to be a uniquely derived character uniting the Ovulidae and Cypraeidae. The feeding specializations of the Ovulidae and associated radular modifications distinguish them from the Cypraeidae. The fused jaws of the Lamellariidae appear to be a modification of the distinct jaws of the Triviidae. Based on the above apomorphic characteristics placement of the Triviidae with the Lamellariidae seems to be the more compatible phylogenetic hypothesis.

TABLE 1
Morphology of the Cypraeacea and Lamellariacea.

Character	Triviidae	Lamellariidae	Ovulidae	Cypraeidae
1. vas deferens	d—closed	d—closed	a—open	a—open
2. bursa copulatrix	d—absent	d—absent	a/d—present or absent	a/d—present or absent
3. larva	d—echinospira	d—echinospira	a—veliger	a—veliger
4. osphradium	a—bipectinate	a—bipectinate	d—triradiate	d—triradiate
5. jaws	a—separate	d—united	a—separate	a—separate
6. lateral radular teeth	a—undivided	a—undivided	d—serrate	a—undivided

a—ancestral; d—derived

The status of *Pedicularia* has also been a controversial aspect of the systematics of the Lamellariacea and Cypraeacea. Schilder (1936) considered the Pedicularinae as a subfamily of the Ovulidae (as Amphiperatidae) but later (1966) considered them as a distinct family in the Triviacea. The internal morphology of *Pedicularia* is largely unknown, with the exception of the radula. Schilder's (1966: 31) transfer of *Pedicularia* from the Ovulidae to the Triviacea appears to be largely based on the fact that its placement was altered in *Zoological Record*. Subsequent authors have merely followed Schilder's placement of *Pedicularia* in the Triviacea.

The fact that *Pedicularia* possesses a trifold osphradium suggests that it is allied to the Cypraeacea. It has none of the derived features uniting the Lamellariacea, although the larval stage remains unknown. The accessory

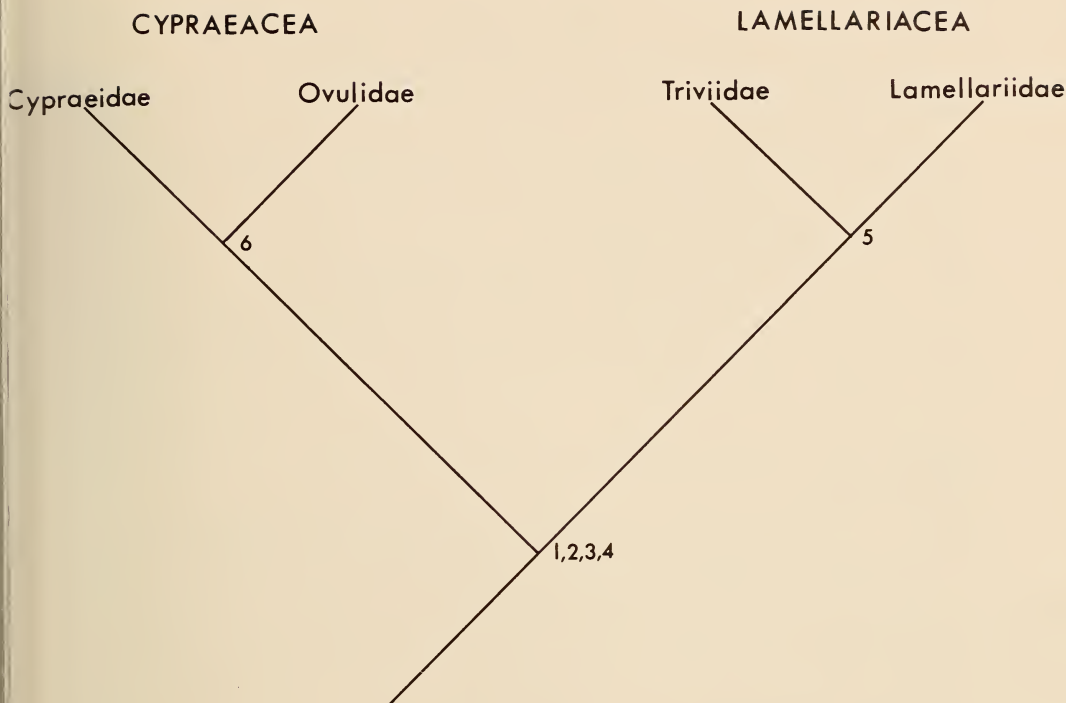


Fig. 35. Phylogeny of the Cypraeacea and Lamellariacea.
(Numbers refer to characters listed in Table 1.)

prostate described here for *Pedicularia* has not been previously observed in any other prosobranch. It may serve as a unique modification separating the Pediculariidae from the Ovulidae. However, no morphological information is available on other *Pedicularia* species and *Cyphoma* is the only ovulid for which details of the morphology are known (Ghiselin & Wilson 1966). Until the morphological variability of these taxa is more completely understood we prefer to retain *Pedicularia* in the Ovulidae.

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ABBREVIATIONS

a	ampulla	dd	digestive diverticulum
al	albumen gland	dg	digestive gland
an	anus	e	eye
bc	bursa copulatrix	eg	oesophageal gland
bm	buccal mass	f	foot
c	cerebral ganglion	h	heart
ct	ctenidium	hg	hypobranchial gland

i	intestine	pr	prostate
j	jaw	ra	radula
k	kidney	rs	receptaculum seminis
m	mantle	s	siphon
me	membrane gland	sb	subintestinal ganglion
mu	mucous gland	sg	sperm groove
od	oviduct	sp	supraintestinal ganglion
oe	oesophagus	st	stomach
os	osphradium	t	testis
ov	ovary	te	tentacle
p	penis	v	visceral ganglion
pe	pedal ganglion	♀ a	female aperture
pl	pleural ganglion		

NOTE

While this paper was in press Burgess (1985) was published, in which *Cypraea lisetae* Kilburn, 1975, was synonymized with *Pustularia maricola* Cate, 1976. The range of *C. lisetae* is thus extended to the Philippines and Solomon Islands, so that it can no longer be regarded as endemic to southern Africa.

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